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HYPERIID AMPHIPODS AS CRUSTACEAN PARASITOIDS ASSOCIATED WITH GELATINOUS ZOOPLANKTON

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INTRODUCTION

A morphological comparison between hyperiid and gammarid amphipods lead Pirlot (1932) to the hypothesis that hyperiids represent an artificial group bringing together the descendants of different lineages of amphipods. Moreover, for Pirlot their convergent hyperiidean form was the result of their association with zooplanktonic hosts. Besides the morphological arguments, Pirlot advanced some biological observations supporting this interpretation: the well-known association of *Hyperia galba* with medusae, the curious behaviour of *Phronima sedentaria* digging 'barrels' in tunicates, and several instances of 'symbioses' (the amphipod being found still hooked to its host) reported by taxonomists studying preserved samples from oceanographic expeditions.

Now almost fifty years have elapsed since Pirlot's study, and evidence of associations has accumulated. A little experimental work has also shed some light on their biological nature. In Villefranche, more than 15 years of observation of live Mediterranean plankton convinced me that every hyperiid species has a parasitic way of life (Laval, 1974b). Recently, Harbison, Biggs & Madin (1977), using SCUBA diving, found direct proof of association *in situ*, and made a similar claim.

In fact, there are a number of biological peculiarities supporting and even extending Pirlot's well-founded insight. His hypothesis could now be re-stated in the following form: hyperiid amphipods are the descendants of benthic crustaceans which have developed a benthic-like existence on the pelagic substratum provided by gelatinous animals of the zooplankton. This paper is devoted to the exploration of the implications of this assertion and its importance for biologists and oceanographers.

OBSERVATION OF HYPERIID ASSOCIATIONS

Hyperiids are pelagic amphipods, not found close to the shore except when great depths are in the proximity, as in Naples and Villefranche in the Mediterranean Sea. Usually an oceanographic vessel is necessary for their collection, with obvious limitations for behavioural studies. In such conditions, the hyperiids can only be either observed on board or brought

back alive to the nearest laboratory. Recently, however, direct information was obtained by observation and hand collection *in situ* by SCUBA divers, providing valuable data on hyperiid associations.

HAND COLLECTION AND *IN SITU* OBSERVATIONS

Underwater observations establish beyond doubt the reality of an hyperiid association. In this way, Madin & Harbison (1977), Harbison, Biggs & Madin (1977), and Harbison, Madin & Swanberg (1978) provided indisputable proof of numerous associations. This technique also allows for the capture of the host in an undamaged state, and thus observation and rearing experiments in the laboratory. The small size of the hyperiids, in most cases, prevents in effect identification to the species level, and limits the *in situ* observation to a few facts, such as position on the host or number of amphipods per host. Although much better than net collection, SCUBA sampling has its own limitations: very small or very fast hyperiids (and hosts) may still remain unnoticed (Hamner *et al.*, 1975); moreover it is limited to the upper 30 m (night-diving could extend the value of the technique with migrating animals, as advocated by Harbison *et al.*, 1977).

Related to SCUBA diving, observation from underwater submersibles has a potential for studying associations in the deeper layers. Franqueville (1970) spotted some hyperiid species from the diving saucer SP 350, but a collecting device such as the "slurp gun" (used by Madin & Harbison, 1978) is needed to capture macroplanktonic animals for subsequent discovery and identification of parasites. Future work with these samplers should reveal new associations which are below the operational range of divers.

Direct observations are sometimes possible from small boats used in areas with nearshore oceanic fauna. In Villefranche, with a bucket or a handle net, it is possible to collect salps, ctenophores, siphonophores or pyrosomes lying close to the surface, and to bring them to the laboratory within 30 min. Some observations shown in Table II (see p. 23) were gathered in this way.

PLANKTON NET COLLECTION

Associations of juvenile and adult hyperiids with their hosts are usually broken off by the strong turbulences developing in the plankton net bucket. Juvenile *Lestrigonus schizogeneios* frequently leave their host (a Leptomedusa) when the rearing jar is only slightly touched (unpubl. obs.). Although rearing conditions in small vessels probably increase their sensitivity, it is nevertheless likely that most hyperiids similarly leave their hosts when caught by nets.

There are, however, some situations when the hyperiid does not, or cannot, leave its host. Larvae of many species have no swimming appendages but are provided with strong hooking dactyls. In the case of *L. schizogeneios*, the larvae are laid by the female into gonads which later regenerate, or inside the manubrium of the medusa (Laval, 1972); they are thus protected against turbulences in the net. For juveniles or adults, the first reaction of the amphipod when struck by the net is probably to secure its grip on the host. If the trawling duration is short (5 min) or if the association is caught shortly before hauling up, the hyperiid may remain on the host. In fact it is not

infrequent to observe associations in the plankton brought back alive to the laboratory. It then remains to ascertain that it was not accidental: in the jar the amphipod could grasp anything providing a substratum. The "association" of *Phronima* larvae with *Acanthephyra* embryos reported by Gordon (1968) is obviously an artefact of this kind. It is only by repetition of observations, rearing experiments or discovery and identification of larvae on hosts that one can be sure of the reality of an association found in a live plankton sample.

Preservation of the catch with formalin causes violent movements of the amphipods which frequently break off the association. Despite this, it is still possible to find amphipods remaining within their hosts, prisoners of natural cavities or hooked to the tissues. Numerous associations found in this manner have been reported in the literature.

LABORATORY METHODS

For a good understanding of the nature of an hyperiid association, rearing of both the amphipod and its host for prolonged periods is necessary. Keeping a healthy host in the laboratory (especially with such delicate zooplankton as siphonophores or salps) is then the major problem. Progress in understanding hyperiid biology will depend on success which will be attained in the culture of macroplanktonic animals.

Obtaining the host in good condition is a key factor for subsequent rearing. Sampling by SCUBA divers is a much better starting point than sampling with a plankton net. For example, Leptomedusae of the genus *Phialidium* caught by nets are damaged and do not resemble intact living specimens; when they are kept, however, a few days in the laboratory with enough food they revert to their normal appearance (Laval, 1972).

When food is scarce or inadequate for the host, a change in feeding behaviour may occur in the amphipod; this important point will be discussed later. The hyperiid alone (when, for instance interest focuses on growth) can be reared without the host, on a diet different from its natural food and more suitable for laboratory work. Phronimids were thus fed with small pieces of mussel mantle (Laval, 1975a), or with bits of benthic molluscs or adult *Artemia salina* (Richter, 1978); *Parathemisto gaudichaudii* eats *Artemia* nauplii (Kane, 1963b; Sheader & Evans, 1975), and *Hyperoche medusarum* was fed with herring larvae (Westernhagen, 1976).

Rearing containers are inevitably confined by walls, and it is difficult to prevent the animals from coming into contact with them; this disturbs the association and renders the host more susceptible to bacterial attacks. Still more harmful to hyperiids is the surface film, on which—if their size is small enough—they adhere by their hydrophobe cuticle. Moulting in the surface film results in distorted appendages. Westernhagen & Rosenthal (1976) used a nylon gauze in order to keep the hyperiids from breaking the surface, and a strip of the same gauze hanging vertically provided attachment for the hyperiids. Keeping these gauzes free from bacteria could be a problem. Some hyperiids, like phronimids (Dudich, 1926; Braun, 1954) or *H. medusarum* (Westernhagen, 1976) are at certain stages photonegative; an overhead light was found advantageous to reduce swimming toward the surface in rearing *Phronima sedentaria* (Laval, 1975a).

Hyperiids and their hosts have until now been kept in small jars (from 200 ml to 10 l) with frequently changed sea water. No systems with running water have yet been tried; they may be needed for some host species. Big tanks should prove useful in the future to cope with large or rapid hosts. Transfer into small vessels, however, would still be necessary to observe the animals under the binocular microscope.

HYPERIIDS AND THEIR HOSTS

Recently Madin & Harbison (1977), Harbison, Biggs & Madin (1977) and Harbison, Madin & Swanberg (1978) have greatly extended the list of known hosts. Their observations come from SCUBA dives and thus give indisputable evidence of associations. Harbison *et al.* (1977) also give a list of previously known hosts from the literature, and discuss at some length the generality and specificity of the relationships. Their list is, however, not complete and is sometimes obscured by second-hand citations. Except for the genus *Hyperia* which is dealt with by Thurston (1977), a revised list, incorporating recent references is given here in Table I. A list of unpublished hosts found by the author in Villefranche between 1962 and 1978 (and during a 'Discovery' cruise in the Atlantic in 1966) is also given in Table II. The present state of knowledge will be summarized here, adopting the classification of the hyperiids of Bowman & Gruner (1973).

INFRAORDER PHYSOSOMATA

Superfamily Lanceolidae

Several authors (Stebbing, 1888, p. 1317; Woltereck, 1909, 1927; Pirlot, 1939a; Vinogradov, 1957) hypothetized that Lanceolidae could be associated with coelenterates, but there exists no direct observation except the report by Chevreux (1900) of three specimens of *Lanceola sayana* under and within medusae *(Pelagia)*.

Superfamily Scinoidea

The report by Chun (1899a,b) of *Scina marginata*—as *Fortunata lepisma*—hooked to the nectophores of the siphonophore *Hippopodius* was largely ignored by subsequent workers. Recent observations (Tables I and II) confirm that Scinidae are associated with siphonophores. Nothing is known, however, of the biology of the remaining families.

INFRAORDER PHYSOCEPHALATA

Family Cystisomatidae

Pirlot (1929, 1932) assumed that members of this family were free-living forms because no associations have ever been reported, an argument which is no longer tenable, although we badly lack information on the biology of these large species.

Family Vibiliidae

Associations of members of the genus *Vibilia* are only known with salps (Tables I and II). *V. borealis* was not found with medusae by Bate & Westwood (1868), as reported in Table 9 of Harbison *et al.* (1977). Nothing is known of the biology of *Cyllopus;* members of this genus possess on pereopods 7 the same rounded dactyls used by *Vibilia* to transfer the larvae to the host (Laval, 1963) and thus are likely to be parasitic.

Family Paraphronimidae

Reported with the siphonophore *Dyphies* and *Galeolaria* by Lo Bianco (1909), *Paraphronima crassipes* was found by Harbison *et al.* (1977), by C. Carré (pers. comm.) and by me (Table II) in nectophores of *Rosacea cymbiformis.*

Family Hyperiidae

The literature on associations of the genus *Hyperia* and zooplankton was recently reviewed by Thurston (1977). His review covers all known references, with only minor omissions (*H. galba* and *Medusa (=Aurelia) aurita:* Bovallius, 1889; and *Pelagia perla (=noctiluca):* Tattersall, 1913; and "medusa": Fage, 1933; and *Rhizostoma octopus:* Certain, 1953; and "large Scyphomedusa": Siegfried, 1963—*Hyperia macrocephala* and "medusa" Bovallius, 1889—*H. medusarum* and "Beroe": Vosseler, 1901; and *Rhizostoma cuvieri, Aurelia aurita, Cyanea capillata:* Guiart, 1913). It should be noted incidentally that Thiel (1976) and Thurston (1977) have erroneously quoted a summary of the literature by the present author (Laval, 1972) as original observations of *Hyperia galba* associated with several species of medusae in the Mediterranean. Apart from these little inadvertencies, Thurston's review should be very useful to the reader interested in associations within the genus *Hyperia.* The references in the Appendix 1 of Thurston (1977) will not be reproduced here in Table I.

In his discussion, Thurston (1977) remarked that almost all associations of *Hyperia* species are with medusae, the only exceptions being some reports with ctenophores and a dubious report with a salp (by Verrill & Smith, 1874). In my opinion, the reality of the associations with ctenophores is not well established; none of the records are provided with precise taxonomic documentation. As already noted by Thurston (1977, Appendix 1, Table B, footnote 8) concerning the obviously erroneous identification by Chun (1880) of *H. medusarum,* young *Hyperoche* could well have been confused with *Hyperia.* More data are required before ascertaining the reality of associations of the genus *Hyperia* with ctenophores.

The genus *Hyperoche* is found on medusae and ctenophores. *H. medusarum* is in most cases associated with medusae, but has sometimes been found on ctenophores (Stephensen, 1923; Brusca, 1970; Evans & Sheader, 1972; Flores & Brusca, 1975). All other species of *Hyperoche* have so far been found with ctenophores (Tables I and II). The multiplicity of hosts reported by Senna (1906) seems to pertain to different hyperiid genera.

Species of the genus *Lestrigonus* have been found only on medusae. The report by Alvarado (1955) of *L. schizogeneios* on the ctenophore *Lampetia*

pancerina is not corroborated by any taxonomic evidence; juvenile *Hyperoche* which are the usual parasites of *Lampetia pancerina* in the Mediterranean (Table II) could well have been confused with this species.

The genus *Hyperietta* has been found by Harbison *et al.* (1977) and me (Table II) associated with polycystine radiolarians of the suborder Collodaria. Hyperiids assigned to *Hyperia,* but referable to *Hyperietta,* were long ago reported by Brandt (1885) as parasites of the radiolarians *Myxosphaera coerula* and *Collozoum pelagicum.* As many small crustaceans are captured by the radiolarians and included in vacuolae, it is not surprising that the hyperiids which are buried in the ectoplasma have escaped the attention of zoologists.

No hosts are reported in the literature for *Hyperioides.* In Villefranche I found in three preserved plankton samples and one live sample juveniles and protopleon larvae of *H. longipes,* in the anterior and posterior nectophores of the siphonophore *Lensia conoidea.* Single nectophores harboured up to four amphipods. The hyperiids found in the live siphonophore were kept for seven days, permitting the observation of the metamorphosis of some protopleon larvae to easily identifiable juveniles, with the characteristic orange colour of the eyes. I also found, in a preserved sample, an anterior nectophore of *Chelophyes appendiculata* with three protopleon larvae possibly belonging to the same species.

Iulopis loveni has been observed by Harbison *et al.* (1977) on the medusa *Pandea conica.* This is the only record for this genus.

The host of *Bougisia ornata,* a Leptomedusa of the genus *Phialidium,* does not seem to belong to the same species as the *Phialidium* with which *Lestrigonus schizogeneios* is associated (Laval, 1966). *Bougisia ornata* may, however, be reared in the laboratory with the latter medusa. Identification of medusae referred to the genus *Phialidium* and also the corresponding hydroids is still not satisfactorily resolved (Kubota, 1978).

In spite of a few early reports of hyperiids of the genus *Parathemisto* associated with medusae (Norman, 1869; Vosseler, 1901; Steuer, 1911; Renshaw, 1965), this genus was considered free-living by most authors (Pirlot, 1932; Dunbar, 1946, 1957; Siegfried, 1965; Kane, 1963b, 1966, among others). Van Zyl (1960) stated that juvenile *Themisto* (referred to *Parathemisto gaudichaudii* by Siegfried, 1965) are among the main diet components of salps off South Africa. It is now evident (see Madin, 1974) that salps cannot feed on amphipods. On the contrary, as shown by the underwater observations of Madin & Harbison (1977) salps are normal hosts for *P. gaudichaudii.* The genus *Parathemisto* thus appears to be associated both with medusae and salps.

Nothing is known of the symbiotic behaviour of the remaining genera of the family *(Pegohyperia, Hyperiella, Hyperionyx, Themistella* and *Phronimopsis)* although their morphology strongly suggests a parasitic existence.

Family Dairellidae

There are no data in the literature on the behaviour of *Dairella.* I once found in Villefranche one subadult female of *D. latissima* attached to the siphonophore *Forskalia edwardsi.* The latter was caught on the surface with

a bucket. On another occasion my colleague C. Carré brought me a subadult male of *Dairella latissima* attached to the Narcomedusa *Cunina vitrea,* also caught with a bucket.

Family Phrosinidae

Anchylomera blossevillei (as *Phrosina macrophthalma)* is said by Risso (1816, 1826) to be found in pyrosomes (and this is repeated in Carus, 1885). Daniel (1973) reported *Primno* sp. in the posterior nectophore of the siphonophore *Abylopsis tetragona.* The position of the hyperiid in his rough drawing does not rule out the possibility of a passive introduction during sample manipulations. *Anchylomera blossevillei* was given as prey, not parasite, for the siphonophore *Forskalia tholoides* by Biggs (1977) and Harbison *et al.* (1977). Bowman (1978) pointed out that the morphology of the dactyls of pereopods 7 strongly suggests a rôle similar to that in *Vibilia,* where they are used to transfer the larva to the host.

TABLE I

List of associations reported in the literature (except for Hyperia *which can be found in Thurston, 1977): C, ctenophore; H, heteropod; M, medusa; P, pteropod; R, radiolarian; S, siphonophore; T, tunicate.*

Hyperiid amphipods	Hosts	References
Lanceolidae		
Lanceola sayana	*Pelagia* (M)	Chevreux, 1900
Scinidae		
Scina marginata	*Hippopodius* (S)	Chun, 1889a,b
Scina sp.	*Sphaeronectes gracilis* (S)	Carré, 1968
Scina sp.	Siphonophores	Harbison *et al.*, 1977
Vibiliidae		
Vibilia jeangerardi	*Salpa maxima* (T)	Marion, 1874
V. jeangerardi	*Salpa maxima* (T)	Chevreux, 1892
V. robusta	Salps	Stephensen, 1918
V. viatrix	Salps	Chevreux & Fage, 1925
V. robusta	*Salpa tilesii (=Tethys vagina)* (T)	Behning, 1927
V. pyripes	Salp	Barnard, 1930
V. robusta	Salp	Chevreux, 1935
V. armata, V. propinqua	*Thalia democratica, Salpa fusiformis, Ihlea punctata* (T)	Laval, 1963
V. viatrix	*Pegea socia, P. confoederata, Salpa maxima, S. cylindrica* (T)	Madin & Harbison, 1977
V. propinqua	*Pegea confoederata, Salpa cylindrica, S. maxima* (T)	Madin & Harbison, 1977
V. pyripes	*Iasis zonaria* (T)	Madin & Harbison, 1977
V. jeangerardi	*Salpa maxima* (T)	Madin & Harbison, 1977
V. stebbingi	*Salpa fusiformis, S. maxima, Cyclosalpa polae* (T)	Madin & Harbison, 1977
V. chuni	*Cyclosalpa polae, Salpa maxima* (T)	Madin & Harbison, 1977
V. kroyeri	*Salpa maxima* (T)	Madin & Harbison, 1977

TABLE I—*continued*

Hyperiid amphipods	Hosts	References
Vibilia sp. A	*Pegea socia, P. confoederata, Salpa cylindrica* (T)	Madin & Harbison, 1977
Paraphronimidae		
Paraphronima crassipes	*Dyphies, Galeolaria* (S)	Lo Bianco, 1909
P. crassipes	*Rosacea cymbiformis* (S)	Harbison *et al.*, 1977
Hyperiidae		
Hyperia: see Thurston, 1977		
Hyperoche martinezii	*Beroe silva* (C)	Müller, 1864
H. lutkeni	*Beroe* sp. (C)	Vosseler, 1901
H. mediterranea, H. picta	*Carmarina* (M), *Abyla* (S), *Beroe* (C), *Salpa* (T)	Senna, 1906
H. mediterranea	*Beroe forskali* (C)	Krumbach, 1911; Steuer, 1911
H. tauriformis (=H. kroyeri)	*Bolina* (C)	Tattersall, 1913
H. medusarum	*Beroe forskali* (C), *Aurelia aurita* (M), medusae	Stephensen, 1923
H. medusarum	*Aurelia aurita* (M)	Schellenberg, 1942
H. mediterranea	*Beroe forskali* (C)	Trégouboff & Rose, 1957
H. medusarum	*Tima formosa* (M)	Bowman *et al.*, 1963
H. medusarum	*Pleurobrachia bachei* (C)	Brusca, 1970
H. medusarum	*Pleurobrachia pileus* (C)	Evans & Sheader, 1972
H. kroyeri	*Beroe cucumis, Pleurobrachia pileus* (C)	Sheader, 1973
H. mediterranea	*Pleurobrachia bachei* (C)	Hirota, 1974
H. medusarum, H. mediterranea	*Pleurobrachia bachei* (C)	Flores & Brusca, 1975
H. medusarum	*Tiaropsis, Sarsia, Phialidium, Polyorchis* (M)	Westernhagen, 1976
H. mediterranea	*Beroe cucumis* (C)	Harbison *et al.*, 1977
H. mediterranea	*Leucothea multicornis* (C)	Harbison *et al.*, 1978
H. mediterranea	*Ocyropsis maculata* (C)	Harbison *et al.*, 1978
H. picta	*Cestum veneris* (C)	Harbison *et al.*, 1978
Lestrigonus schizogeneios	*Lampetia pancerina* (C)	Alvarado, 1955
L. schizogeneios	*Phialidium* sp. (M)	Laval, 1968a
L. schizogeneios	*Phialidium, Leuckartiara nobilis, Liriope tetraphylla* (M)	Laval, 1972
L. schizogeneios	*Aequorea* sp. (M)	Harbison *et al.*, 1977
L. bengalensis	*Eirene pyramidalis* (M)	Harbison *et al.*, 1977
L. crucipes	*Pelagia noctiluca* (M)	Harbison *et al.*, 1977
Hyperietta sp. (as *Hyperia*)	*Myxosphaera coerula, Collozoum pelagicum* (R)	Brandt, 1885
Hyperietta stebbingi	*Collozoum* sp. (R)	Harbison *et al.*, 1977
H. stephenseni	Radiolarian colony	Harbison *et al.*, 1977
Iulopis loveni	*Pandea conica* (M)	Harbison *et al.*, 1977
Bougisia ornata	*Phialidium* sp. (M)	Laval, 1966
Parathemisto gaudichaudii	*Aurelia* (M)	Norman, 1869
P. gaudichaudii	*Umbrosa (=Discomedusa) lobata* (M)	Trégouboff & Rose, 1957
P. pacifica	*Calycopsis nematophora* (M)	Renshaw, 1965
P. gaudichaudii	*Pegea confoederata* (T)	Harbison, 1976
P. gaudichaudii	*Pegea bicaudata, Pegea* sp., *Salpa* sp., *Iasis zonaria* (T)	Madin & Harbison, 1977

TABLE I—*continued*

Hyperiid amphipods	Hosts	References
Phrosinidae		
Anchylomera blossevillei (as *Phronima macrophthalma)*	Pyrosomes	Risso, 1816, 1826
Primno sp.	*Abylopsis tetragona*	Daniel, 1973
Phronimidae		
Phronima colletti	*Abyla trigona* (S)	Chun, 1889b, 1895
P. colletti	*Diphyes* sp. (S)	Vosseler, 1901
P. curvipes	*Abylopsis tetragona* (S)	Laval, 1968b
P. colletti	*Chelophyes appendiculata* (S)	Laval, 1968b
P. stebbingii	Unidentified barrel	Laval, 1968b
P. pacifica	*Lensia fowleri* (S)	Daniel, 1973
P. colletti	*Salpa aspera* ? (T)	Harbison *et al.*, 1977
P. pacifica	*Abylopsis tetragona* (S), *Salpa aspera* ? (T)	Harbison *et al.*, 1977
P: sedentaria	*Thalia democratica, Salpa fusiformis, Ihlea punctata, Pyrosoma atlanticum* (T)	Laval, 1978
Phronimella elongata	In barrel	Mayer, 1879
Lycaeopsidae		
Lycaeopsis themistoides	*Monophyes* or *Dyphies* (S)	Stephensen, 1925
L. themistoides	*Chelophyes appendiculata* (S)	Laval, 1965
L. themistoides	*Diphyes dispar* (S)	Harbison *et al.*, 1977
Pronoidae		
Paralycaea gracilis	*Aglantha* ? (M)	Stephensen, 1925
Euprone maculata	Salp	Spandl, 1927
Eupronoe ?	*Lilyopsis rosea* (S)	Carré, 1969
Paralycaea newtoniana	*Sulculeolaria monoica, S. chuni, S. quadrivalvis* (S)	Harbison *et al.*, 1977
P. hoylei	*Sulculeolaria quadrivalvis, Nanomia bijuga* (S)	Harbison *et al.*, 1977
P. gracilis	*Sulculeolaria chuni, S. monoica, Agalma clausi* (S)	Harbison *et al.*, 1977
Sympronoe parva	*Rosacea cymbiformis* (S)	Harbison *et al.*, 1977
Eupronoe minuta	*Agalma elegans* (S)	Harbison *et al.*, 1977
Encysted juveniles	*Forskalia tholoides, F. edwardsi, Agalma clausi, A. okeni, Athorybia rosacea* (S)	Harbison *et al.*, 1977
Juveniles	*Stephanophyes superba* (S), *Aequorea* sp. (M)	Harbison *et al.*, 1977
Lycaeidae		
Lycaea ochracea	Salps	Dana, 1853
Thamneus (as *Daira*?) *debilis*	Medusae	Dana, 1853
Lycaea pulex	Salps	Marion, 1874
L. robusta	Salps	Caruş, 1885
Brachyscelus sp.	*Bolina* sp. (C)	Chun, 1887
Lycaea pulex	*Salpa maxima* (T)	Chevreux, 1892
Pseudolycaea pachypoda	Pyrosomes	Chevreux, 1892
P. pachypoda	Salps, pyrosomes	Chevreux, 1900
Lycaea pulex	*Salpa maxima* (T), pyrosomes	Chevreux, 1900
Brachyscelus crusculum	Salps	Stephensen, 1923

TABLE I—*continued*

Hyperiid amphipods	Hosts	References
B. crusculum	Salps	Stephensen, 1925
Thamneus platyrrhyncus	Medusae	Stephensen, 1925
Lycaea pulex	*Salpa maxima* (T), pyrosomes	Chevreux & Fage, 1925
Pseudolycaea pachypoda	*Salpa maxima* (T), pyrosomes	Chevreux & Fage, 1925
Lycaea pulex	Salps	Pirlot, 1939a
Brachyscelus crusculum	Medusae	Pirlot, 1939a
Lycaea pulex	*Salpa maxima* (T)	Trégouboff & Rose, 1957
Pseudolycaea pachypoda	Salps, pyrosomes	Trégouboff & Rose, 1957
Lycaea pulex	*Cyclosalpa pinnata, Pegea confoederata* (T)	Harbison, 1976
L. pulex	*Cyclosalpa affiñis, C. bakeri, C. pinnata, Helicosalpa komaii, Ihlea punctata, Pegea socia, P. bicaudata, P. confoederata, Salpa cylindrica, S. maxima, Transtedtia multitentaculata* (T)	Madin & Harbison, 1977
L. vincentii	*Pegea confoederata, Salpa cylindrica* (T)	Madin & Harbison, 1977
L. nasuta	*Cyclosalpa affinis* (T)	Madin & Harbison, 1977
L. 'bovallioides'	*Cyclosalpa pinnata, Pegea socia, P. confoederata, Salpa cylindrica, S. maxima* (T)	Madin & Harbison, 1977
Lycaea sp. A	*Cyclosalpa polae, Salpa cylindrica, S. maxima* (T)	Madin & Harbison, 1977
Brachyscelus crusculum	*Cyclosalpa affinis, Iasis zonaria, Pegea socia, Salpa maxima, Thalia democratica* (T)	Madin & Harbison, 1977
Lycaea 'bovallioides'	*Corolla spectabilis* (P)	Harbison *et al.*, 1977
Lycaea sp.	*Gleba cordata* (P)	Harbison *et al.*, 1977
Pseudolycaea pachypoda	*Liriope tetraphylla* (M)	Harbison *et al.*, 1977
Brachyscelus rapacoides	*Aequorea* sp., *Orchistoma* sp., *Leuckartiara* sp. (M), Hydromedusa, *Cavolinia longirostris* (P), tornaria larvae	Harbison *et al.*, 1977
B. crusculum	Leptomedusa, *Aequorea* sp. (M), *Pterotrachea* sp. (H)	Harbison *et al.*, 1977
Brachyscelus sp.	*Orchistoma* sp., *Aequorea* sp. (M), Leptomedusa	Harbison *et al.*, 1977
Thamneus platyrrhyncus	*Pelagia noctiluca* (M)	Harbison *et al.*, 1977
Oxycephalidae		
Oxycephalus similis	Medusae	Carus, 1885
O. piscator	*Leucothea multicornis* (C)	Chun, 1889b
Glossocephalus milne-edwardsi	*Deiopea kaloktensta* (C)	Steuer, 1911; Krumbach, 1911
Tullbergella	? *Cotylorhiza* sp. (M)	Barnard, 1931
Oxycephalus clausi	*Pegea socia, Salpa cylindrica* (T)	Madin & Harbison, 1977
Cranocephalus scleroticus	*Pleurobrachia* sp. (C)	Harbison *et al.*, 1977
Glossocephalus milne-edwardsi	*Bolinopsis vitrea* (C)	Harbison *et al.*, 1977
Oxycephalus clausi	*Ocyropsis maculata* (C), *Pterotrachea hippocampus* (H)	Harbison *et al.*, 1977
Streetsia porcella	Radiolarian colony, *Leucothea* sp. (C), marine snow	Harbison *et al.*, 1977
Cranocephalus scleroticus	Cydippids (C)	Harbison *et al.*, 1978

TABLE I—*continued*

Hyperiid amphipods	Hosts	References
Glossocephalus milne-edwardsi	*Bolinopsis vitrea, Leucothea multicornis, Cestum veneris* (C)	Harbison *et al.*, 1978
Oxycephalus clausi	*Eurhamphaea vexilligera, Mnemiopsis mccradyi, Ocyropsis cristallina, O. maculata, Beroe* sp., *Cestum veneris* (C), medusae, colonial radiolarians	Harbison *et al.*, 1978
O. latirostris	*Eurhamphaea vexilligera, Cestum veneris* (C)	Harbison *et al.*, 1978
O. piscator	*Mnemiopsis mccradyi* (C)	Harbison *et al.*, 1978
Oxycephalus sp.	*Leucothea multicornis, Cestum veneris* (C)	Harbison *et al.*, 1978
Streetsia porcella	*Eurhamphaea vexilligera, Leucothea multicornis* (C)	Harbison *et al.*, 1978
Rhabdosoma whitei	*Beroe* sp. (C)	Harbison *et al.*, 1978
Rhabdosoma sp.	*Beroe* sp. (C)	Harbison *et al.*, 1978
Platyscelidae		
Platyscelus ovoides	*Aequorea* (M)	Risso, 1816
Amphithyrus bispinosus	*Agalma elegans* (S)	Harbison *et al.*, 1977
A. glaber	*Agalma elegans* (S)	Harbison *et al.*, 1977
A. similis	*Chelophyes appendiculata* (S)	Harbison *et al.*, 1977
Tetrathyrus forcipatus	*Agalma clausi* (S)	Harbison *et al.*, 1977
T. forcipatus	*Nanomia bijuga* (S)	Harbison *et al.*, 1977
Parascelidae		
Schizoscelus ornatus	*Bathyphysa sibogae* (S)	Biggs & Harbison, 1976
Thyropus edwardsii	*Bathyphysa sibogae* (S)	Biggs & Harbison, 1976
Schizoscelus ornatus	*B. sibogae* (S)	Harbison *et al.*, 1977
Thyropus edwardsii	*Agalma okeni, Forskalia tholoides, Diphyes dispar, Bathyphysa sibogae* (S)	Harbison *et al.*, 1977
T. sphaeroma	*Stephanophyes superba* (S)	Harbison *et al.*, 1977
T. similis	*Agalma okeni, Athorybia rosacea, Athorybia* sp. (S)	Harbison *et al.*, 1977
Thyropus sp.	*Agalma okeni, Stephanophyes superba, Forskalia edwardsi, Forskalia* sp., *Diphyes dispar, Abyla* sp., *Athorybia rosacea, Athorybia* sp. (S)	Harbison *et al.*, 1977
T. similis	*Athorybia lucida* (S)	Biggs, 1978

Family Phronimidae

Phronimids live in 'barrels', which are shaped from gelatinous hosts open at both ends. Often the barrel is so transformed that distinctive morphological characteristics have been lost. Using multivariate morphometric methods, it was possible to group the barrels of *Phronima sedentaria* into several classes, and then to trace each class back to a host (Laval, 1978). In the Mediterranean Sea, the hosts of *P. sedentaria* can be attributed to several species of salps and the pyrosome *Pyrosoma atlanticum*. Previous references to *Phronima*

sedentaria barrels do not lead to conclusive host identifications (see Laval, 1978).

For *P. atlantica* the situation is no clearer than for *P. sedentaria.* Direct proofs of barrel origin are lacking in the literature, and in addition the identification of juvenile stages if often questionable. For the Villefranche specimens, I have not yet undertaken a systematic analysis such as that on *P. sedentaria,* but a few preliminary conclusions may be drawn from my notes. Characteristic remains can be found on some barrels, leading to the identification of the solitary forms of *Salpa fusiformis* and *Thalia democratica.* The transformation of a blastozooid of *Salpa fusiformis* into a barrel was observed twice in the laboratory. I did not find any *Phronima atlantica* in siphonophores.

It should be noted that males of *P. sedentaria* and *P. atlantica* are also found in barrels (Chun, 1895; Woltereck, 1904a; Dudich, 1926; Harbison *et al.,* 1977; Laval, 1978). The hosts have not been identified, but are likely to be the same as those of young females of corresponding size.

The remaining species of the genus *Phronima* are found in siphonophores and salps (Table I).

The short mention by Mayer (1879) of *Phronimella elongata* inhabiting a barrel has not been noticed by subsequent authors. I found *P. elongata* in barrels on several occasions; a specimen in its barrel, photographed by my colleague C. Carré, is shown in Ehrhardt & Seguin (1978, p. 207). As noted by Mayer (1879), the barrel is highly transparent: it reminds me of an occasion when it took me about one hour to find it in a jar. It is hard to make out even under a binocular microscope. The barrel of *Phronimella* is also very soft and is stretched out by the pereopods of the animal. Its origin is not known. Mayer (1879) said that he was not able to detect the presence of cellulose.

Family Lycaeopsidae

Lycaeopsis themistoides lives in diphyid siphonophores. Harbison *et al.* (1977) found it in the superior nectophore of *Diphyes dispar.* In Villefranche it occurs in the anterior (=superior) nectophore of *Chelophyes appendiculata* (Laval, 1965).

Family Pronoidae

This family is in need of revision (Zeidler, 1978). There seem to be great morphological variations during development, and between males and females. Several species were found mostly in siphonophores by Harbison *et al.* (1977), although there are a few earlier reports in medusae, and even one in salps (see Tables I and II). Juvenile stages are found 'encysted', *i.e.* burrowed in the mesogloea, with no visible connection with the exterior (Harbison *et al.,* 1977).

Family Anapronoidae

The only genus, *Anapronoe,* for which Bowman & Gruner (1973) created the family, is not reported as associated with zooplanktonic hosts.

TABLE II

List of associations found in Villefranche, Mediterranean Sea, with some observations from the northeast Atlantic (Discovery cruise, Oct.–Nov. 1966): unpublished observations only; C, ctenophore; M, medusa; R, radiolarian; S, siphonophore; T, tunicate.

Hyperiid amphipods	Hosts
Scinidae	
Scina marginata	*Hippopodius hippopus* (S)
S. tullbergi	*Sphaeronectes gracilis* (S)
S. unicipes var. *lamperti*	*Ceratocymba sagittata* (S) 'Discovery'
Vibiliidae	
Vibilia armata	*Pegea confoederata* var. *bicaudata* (T)
V. jeangerardi	*Salpa maxima* (T)
V. propinqua	*Pegea confoederata* var. *bicaudata* (T)
V. viatrix	*Pegea confoederata* var. *bicaudata* (T)
Paraphronimidae	
Paraphronima crassipes	*Rosacea cymbiformis* (S)
Hyperiidae	
Hyperietta stephenseni	*Sphaerozoum* sp., *Collozoum* sp. (R)
H. vosseleri	*Thalassoxanthium* sp. (R) 'Discovery'
Hyperioides longipes	*Lensia conoidea* (S)
H. longipes ? (larvae)	*Chelophyes appendiculata* (S)
Hyperoche martinezii	*Bolina hydatina, Beroe forskali* (C)
H. mediterranea	*Lampetia pancerina* (C)
Dairellidae	
Dairella latissima	*Forskalia edwardsi* (S), *Cunina vitrea* (M)
Phronimidae	
Phronima atlantica	*Salpa fusiformis, Thalia democratica* (T)
Phronimella elongata	In barrel of unknown origin
Pronoidae	
Eupronoe minuta	*Apolemia uvaria, Sulculeolaria quadrivalvis* (S)
Lycaeidae	
Brachyscelus crusculum	*Salpa fusiformis* (T)
Brachyscelus sp. juv.	*Leuckartiara octona* (M)
Lycaea pulex	*Salpa maxima, Pyrosoma atlanticum* (T)
Pseudolycaea pachypoda	*Pyrosoma atlanticum* (T)
Thamneus platyrrhyncus	*Pelagia noctiluca* (M)
Tryphana malmi	*Ceratocymba sagittata* (S) 'Discovery'
Oxycephalidae	
Glossocephalus milne-edwardsi	*Leucothea multicornis, Beroe ovata* (C)
Simorhynchotus antennarius	*Geryonia proboscidalis* (M)
Platyscelidae	
Amphithyrus similis	*Chelophyes appendiculata* (S)
Platyscelus serratulus	*Agalma elegans* (S)
Platyscelus sp.	*Pelagia noctiluca* (M)
Parascelidae	
Thyropus typhoides	*Forskalia (edwardsi ?)* (S)

Family Lycaeidae

The need for taxonomic revision, stressed by Zeidler (1978), limits our knowledge of host specificity in this family. This specificity seems, however, to be broad in the light of recent underwater observations made by Madin & Harbison (1977) and Harbison *et al.* (1977). Some species undoubtedly are found on different hosts. From Tables I and II, the range is from salps to medusae, passing by pteropods, heteropods, siphonophores and even ctenophores (but the only observation of Chun, 1887, of *Brachyscelus* with *Bolina* needs confirmation). Whether these hosts are 'obligate' or are nothing more than prey or supports will be discussed later.

Family Oxycephalidae

The genus *Simorhynchotus* is placed by Bowman & Gruner (1973) in the Oxycephalidae, but shows several characteristics of the Lycaeidae (Fage, 1960; Zeidler, 1978). The Oxycephalidae are thus close to the Lycaeidae. Accordingly they seem to exhibit the same kind of behaviour, being found on a diversity of hosts (Tables I and II), of which ctenophores are the most frequently reported (but this is perhaps due to the sampling methods). As in the Lycaeidae they also appear to be in loose association with their hosts.

Families Platyscelidae and Parascelidae

These two families are not very distinct and could well need to be united after revision. The existence of changes in the number of segments of pereopod 7 between successive moults (in *Platyscelus serratulus*, unpubl. obs.), and variation in uropod 2 between specimens in *Tetrathyrus forcipatus*, Zeidler, 1978) call for more investigations on morphological changes before attempting such a revision.

Members of these two families appear to live mostly on siphonophores, but in some cases have been reported with medusae (Tables I and II).

GENERALITY OF ASSOCIATIONS

The associations reported in Tables I and II should not be taken as an authoritative list. They are first and foremost provided to impress the reader, and to convince him that hyperiids are not free-living amphipods. Moreover, although the hosts of several genera, and even families, have not yet been discovered, it would appear permissible to support the inference of Harbison (1976) that "it may well be that all hyperiid amphipods spend some portion of their lives in association with gelatinous zooplankton". The same hypothesis was proposed in my unpublished dissertation (Laval, 1974b). The genera for which no associations are known are indeed not strikingly different from those for which we have some data, and often possess similar grasping organs or other adaptations. A stronger argument for this hypothesis is that hyperiid amphipods are not biologically fitted for a pelagic free-living existence. This point is central to this review and will be fully developed in the following pages.

It seems premature to make conclusions about host specificity (at the level of the whole suborder) from the data in Tables I and II. Some genera, and even families, appear to be restricted to certain host groups, as already noted by Harbison *et al.* (1977). One should, however, keep in mind that the data are sparse; in addition some specificities may not hold in different geographical areas, or for other life stages. In fact the problem of specificity is rather an ecological one, the domain of the potential hosts being the ecological niche for a given hyperiid. We are far from being able to delimitate this domain for any hyperiid species.

THE BIOLOGY OF HYPERIIDS

HOST INFESTATION: THE NECESSITY OF A MATERNAL MEDIATION

If hyperiids are not free-living, at least in the early stages of their lives, they must discover their hosts. This search is more problematical for hyperiids than for parasitic or commensal gammarids, the young of which may find their host, which is in most cases sessile, in the immediate vicinity of the mother. On the other hand, young expelled from a brood pouch into the pelagic environment would have very little likelihood of encountering a host. This could be compensated by the production of a large number of progeny, as in epicaridean isopods. Here, in order to produce numerous young, the body of the female undergoes a drastic transformation changing it into an egg pouch.

In hyperiids no such changes are known. The number of eggs in the brood pouch of hyperiids is greater than in gammarids but still not enormous. It does not exceed 600 in *Phronima sedentaria* (Laval, 1975a; note that the Fig. 1 was misprinted, see Laval, 1975b). This species is one of the biggest hyperiids. *Cystisoma* species are still bigger, but their egg number is unknown; egg numbers in amphipods are roughly correlated with female size. Except for *Phronima* only a few counts were reported: up to 200 eggs in *Parathemisto japonica* (Behning, 1939), 20 to 60 in *P. pacifica* (Bowman, 1960), 10 to 200 in *P. gaudichaudii* (Sheader, 1977), 60 to 450 in *Hyperia galba* (Metz, 1967), up to 228 in *Lycaea pulex* (Harbison, 1976), about 10 to 150 in different species of Oxycephalidae (Fage, 1960). I found approximately 120 larvae in the marsupium of *Vibilia armata* and *V. propinqua*, and 70 in *V. jeangerardi* (unpubl. data). Many species are smaller than the above and are not likely to carry many more eggs; 36 larvae were counted in the marsupium of the small species *Lestrigonus schizogeneios* (Laval, 1968a), and between 48 to 94 in *Hyperoche medusarum* (Westernhagen, 1976). These egg numbers are clearly not compatible with a random search for hosts by the progeny. In other words, such egg production cannot counterbalance the hazards of an early pelagic life.

To ensure the continuation of the species in the discontinuous substratum which hosts scattered in the ocean represent, a female hyperiid must, therefore, be responsible for the dissemination of her limited progeny. With the swimming capacity of a fully grown animal, she can seek hosts with the same efficiency as she searches for food. Moreover she can ensure that each of her young is provided with the correct host.

DEPOSITION OF THE PROGENY ON THE HOST: THE DEMARSUPIATION

In gammarids and a certain number of hyperiids, the hatching stage does not differ fundamentally from a miniature adult; proportions and segmentation are of course different, but the general form is retained. It is classically said that amphipods undergo a direct or 'epimorphic' embryonic development. In many hyperiids there exist, however, specialized larval stages, the morphology of which is related to host deposition. These stages are 'larval' in the sense that the shape is different from the juvenile form, the posterior part of the body is in an embryonic state (incomplete segmentation and lack of appendages), and often some cheliform extensions are present which will subsequently disappear. The stage corresponding to the hatching stage of gammarids will be attained only after metamorphosis. This develoment is thus indirect or 'anamorphic'; it will be detailed in the following section.

Whether the newly born hyperiid hatches as larva or juvenile, it is transferred from the brood pouch, or marsupium, of the female into the host, following some special behavioural sequences. I propose to name 'demarsupiation' the process of removing the young from the marsupium and their deposition on the hosts by the female. The demarsupiation is not easy to observe. It calls for watching the female on the host under a stereomicroscope. Moreover the process is fast, some sequences taking only a few seconds. It is best studied with the aid of a videotape recorder. Fortunately during this process the female does not seem to be disturbed by laboratory handling.

Examples of demarsupiation

There are few observations of demarsupiation recorded in the literature. It was described in *Vibilia armata* (Laval, 1963) and in *Lestrigonus schizogeneios* (Laval, 1972). Sheader (1977) reported on the "release behaviour" of *Parathemisto gaudichaudii* but, as the female was not observed on a host, there are some reasons to suspect that this behaviour was somewhat atypical. This point will be discussed below. Harbison, Madin & Swanberg (1978) also reported deposition of young on the surface of ctenophores by *Glossocephalus milne-edwardsi,* but gave no details of the process.

In *Vibilia armata* (Laval, 1963) the female attaches herself to the surface of the host, a salp, and waits for the apparition of a larva at the posterior end of the marsupium. At regular intervals she can be seen rapidly curving her abdomen so that the tip of the uropods touches the surface of the salp. She cannot, however, extract the larvae from her brood pouch. The fast beating of the pleopods, which produces a current running in a tailward direction may help the larvae to find their way to the posterior outlet of the marsupium. When a larva emerges from the brood pouch, the urosome folds forwards and the larva, seized between the peculiar rounded dactyls of pereopods 7, is driven on to the host surface, sliding between the pleopods and the outer surface of the marsupium.

In *Lestrigonus schizogeneios,* the demarsupiation involves a more complex sequence of events (Laval, 1972). When the female clings to the host, a Leptomedusa of the genus *Phialidium,* the latter contracts violently

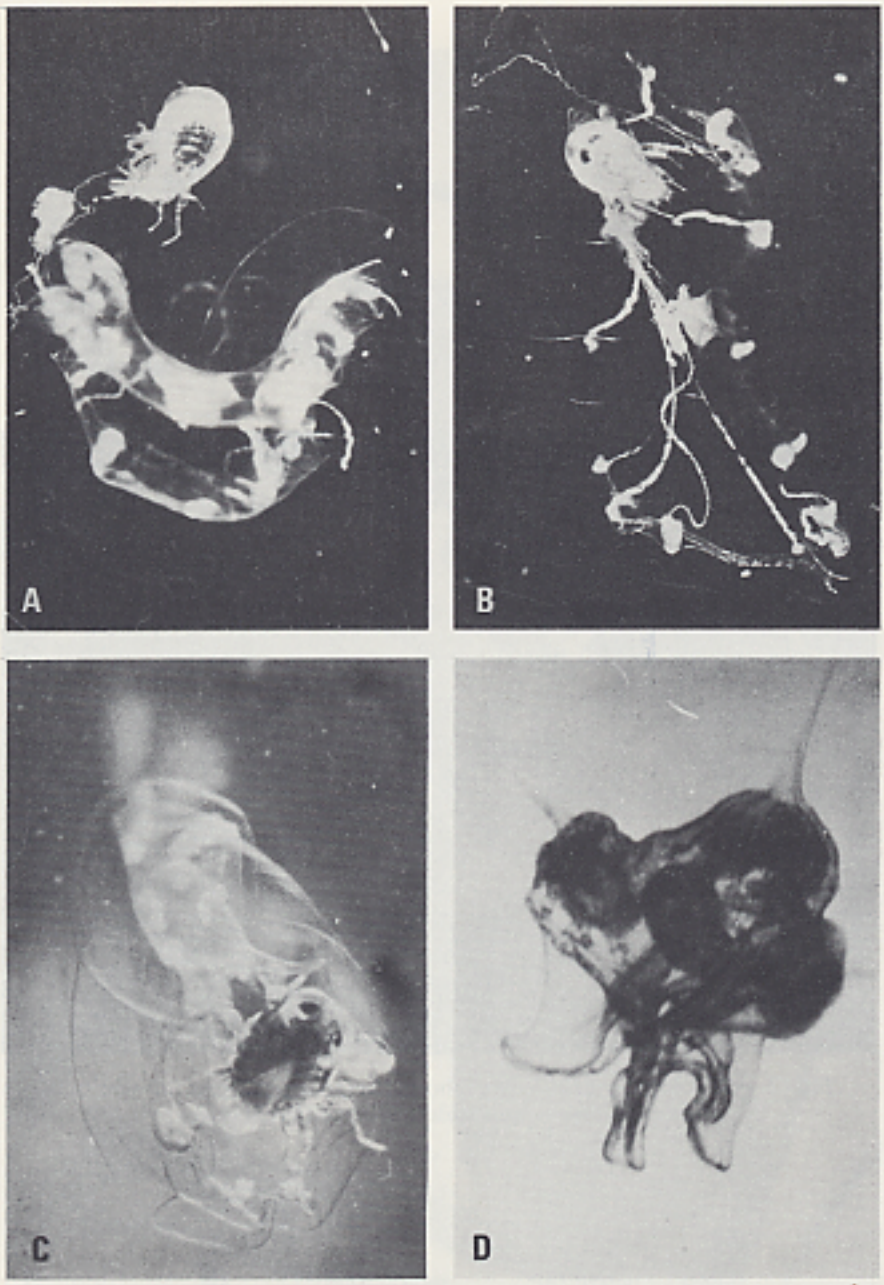

Fig. 1.—"Demarsupiation" (transfer of the larvae from the brood pouch to the host) in *Lestrigonus schizogeneios*: A, the female grasps the host, a Leptomedusa of the genus *Phialidium*, which violently contracts under the prick of the dactyls ; B, the female has found the umbrella slit and enters the subumbrella; C, a larva, emerging from the marsupium, is rolled to the manubrium; D, four larvae may be seen inside the manubrium; the diameter of the medusa is about 10 mm.

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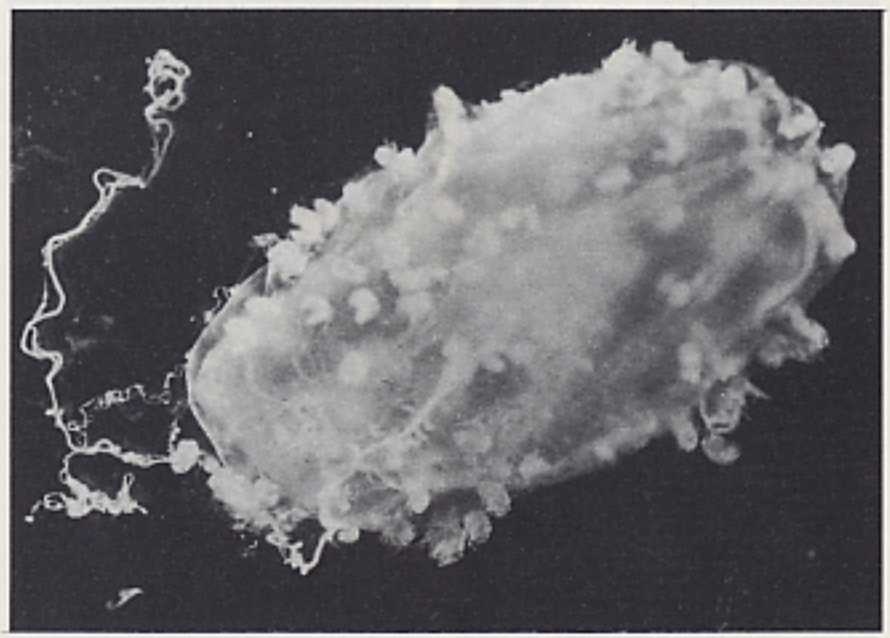


Fig. 2.—A specimen of the ctenophore *Lampetia pancerina* infested by numerous *Hyperoche mediterranea* at different stages.

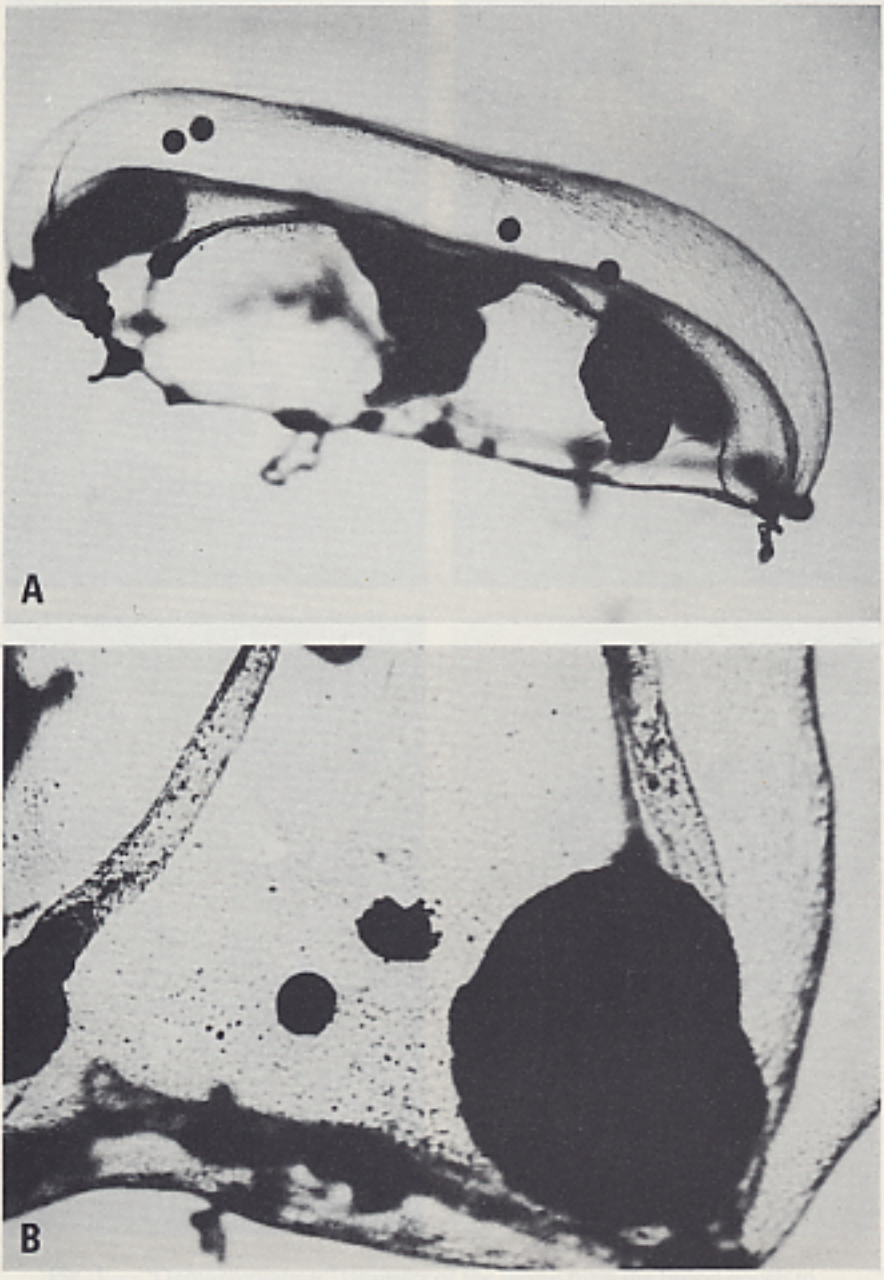


Fig. 3.—Oviposition in *Bougisia ornata*: A, a Leptomedusa of the genus *Phialidium* with four eggs of *Bougisia ornata* included in the umbrella by the female (largest diameter of the eggs is 0·2 mm); B, an egg and a larva just hatched.

as it is punctured by the dactyls (Fig. 1A). The hyperiid then rolls the contracted spherical *Phialidium* until she discovers the umbrellar slit, and then enters the subumbrella (Fig. 1B). It can be shown that this is a stereotyped element of behaviour: if a ball made of umbrellar tissue (obtained by cutting off gonads and manubrium) is given at that stage to the female, she turns the sphere endlessly between the gnathopods and the other pereopods. When the female has penetrated into the subumbrella, she does not deposit her larvae at random: she goes either to a gonad or to the manubrium. If she finds a gonad smaller than a larva, she continues her search until she discovers a bigger gonad or the manubrium. The organ is then opened with the gnathopods (in the case of a gonad, it is first split by the mouth-parts), and the female waits for the apparition of a larva at the posterior end of the marsupium, as in *Vibilia.* When a larva emerges, it is rolled between the outer surface of the marsupium and the anterior face of pleopods 1 with a brushing action of the latter, until it can be seized by the gnathopods, which transfer it to the gonad or the manubrium (Fig. 1C). The lips of the wounded gonad soon join and weld; the larva stays in the gonad until the regeneration can no longer balance tissue removal. In the manubrium the larva may remain (undigested) till the first juvenile stages (Fig. 1D), but may also be seen leaving and re-entering the manubrium. Between 1 to 5 larvae (generally 1 to 3) are transferred on to the host in this way. The female then leaves the *Phialidium,* exhibiting a characteristic 'escape reaction'.

In *Hyperoche mediterranea,* the demarsupiation does not differ very much from that in *Lestrigonus schizogeneios* (unpubl. obs.). I only observed it in one occasion, while in *L. schizogeneios* the behavioural sequences were repeatedly observed. *Hyperoche mediterranea* is found in Villefranche on the ctenophore *Lampetia pancerina.* One individual host may harbour up to about 50 *Hyperoche,* at different stages, obviously the result of several infestations (Fig. 2). The female hooks herself on the ctenophore surface by pereopods 5 to 7, as already observed by Flores & Brusca (1975) in this species and in *H. medusarum.* For the demarsupiation, she swings down, facing the host, and digs a small cavity on the surface with her gnathopods. Then she folds her abdomen, and rubs the marsupium with the anterior face of pleopods 1, as in *Lestigonus schizogeneios.* As in this species, the larva is conveyed to the host by the pleopods, relayed by the gnathopods, which put it in the cavity.

In *Bougisia ornata* (unpubl. obs.) the demarsupiation is extraordinary in the sense that it is an oviposition. The following observations were made in 1966, but I did not publish them, hoping subsequently to get a more complete account. As I did not succeed in finding more data, I take the opportunity of this review to report on this behaviour. *B. ornata* is associated in Villefranche with a Leptomedusa of the genus *Phialidium* (Laval, 1966), distinct from the species parasitized by *Lestrigonus schizogeneios.* I put in the same jar a specimen of this *Phialidium* (remarkable by its deep green manubrium) and an ovigerous female of *Bougisia.* The jar was left unobserved for two days. When it was again put under the stereomicroscope, I discovered six eggs included in the umbrella, similar to those in the marsupium of the female, and showing the beginning of segmentation. On the same day, I obtained another green *Phialidium* in a

live plankton sample, and upon examination it was found to carry two eggs in the umbrella, similar to the others, with a diameter of about 0·2 mm. These green *Phialidium* are rare in the plankton (which probably explains why *Bougisia* are also scarce), so I put the ovigerous female in the same vial as the *Phialidium* with two included eggs. The female soon attached herself to the medusa, then entered the subumbrellar slit of the contracted medusa. She began to stretch the subumbrellar tissue with the gnathopods, biting the mesogloea with the mouthparts. The second pair of gnathopods were used to plunge into the incision to bring the bottom of the cavity near the surface, where the first pair secured it. This required several gnathopod interventions. When the incision became deep enough, with its bottom taken back near the surface, the female curved her pleon, and with the brushing action seen in the preceding species, rolled an egg to the first pair of gnathopods, pushed it in the cavity, and released the grip of the second pair of gnathopods. The egg was thus included deep in the umbrella (more than half way down) by the elastic retraction of the bottom of the cavity (Fig. 3A). The female repeated this oviposition on another occasion, in exactly the same manner. The eggs developed normally in the umbrellar tissue, and hatched after seven days (Fig. 3B). The larvae (a pantochelis stage, with undifferentiated abdomen) progress in a backward direction in the mesogloea. They soon gained the exterior of the subumbrella and ate the gonads. The development was followed in the laboratory from the pantochelis stage to the first juvenile stage, which was reached through three protopleon stages.

In *Lestrigonus schizogeneios,* the larvae do not appreciably increase in size as long as they remain in the marsupium (Laval, 1968a). The metamorphosis changing them from protopleon larvae to first stage juveniles only takes place when they begin to feed on the host tissues. The same thing may be observed in *Vibilia.* As the larvae do not moult and do not increase in size while in the marsupium, they are not mechanically forced out of the brood pouch, allowing the female the possibility of a long search for hosts.

In other hyperiids, such as *Phronima sedentaria,* the larvae moult in the brood pouch (Laval, 1975a). This is not fatal for the larvae because they are demarsupiated while the female is in the barrel. The larvae dislodged by the size increase of the brood may thus settle on the barrel wall. There are three protopleon stages in *P. sedentaria,* but only stages I and II are found in the marsupium. The numerous eggs do not develop strictly synchronously, so that stages I and II may be found together in the marsupium. Sometimes the brood pouch is emptied all at once, at other times there are several batches of larvae. I observed the demarsupiation only once; this observation should be repeated because the living conditions of such a big amphipod in a small vial under a stereomicroscope are not very natural. The female was seen spreading the last two pairs of oostegites with gnathopods 1 and 2, which were crossed under the sternites. The larvae, jammed in the 'elbow' formed by the basis and the following segments of the gnathopods, were then combed with a headward movement of the latter, until they fell in the barrel, where they secured their grip with their very sharp dactyls. An active participation of the larvae seems necessary, because unhatched eggs are not evacuated whereas larvae are.

Demarsupiation in *Phronima* has several features in common with the "release behaviour" described by Sheader (1977) for *Parathemisto gaudichaudii*. The increase of egg size, the moulting of the juvenile inside the marsupium, and the active participation of the juveniles are similar. The expulsion of the juveniles from the marsupium is not accomplished in *Parathemisto* with the aid of the gnathopods, but by a scraping action of the uropods. In Sheader's opinion the juveniles are released to be free-swimming in the ocean. Juveniles are nevertheless found attached to hydromedusae (Sheader & Evans, 1975), and this host-parasite relationship was confirmed by Madin & Harbison (1977), who found *P. gaudichaudii* on salps. It seems reasonable to postulate that juveniles of *P. gaudichaudii* are released by the female on to a host.

LIMITATION OF THE NUMBER OF PARASITES PER HOST

When the size of the host is small relative to the hyperiid size, as in *Lestrigonus schizogeneios* which parasitizes small Leptomedusae, the female herself limits the number of larvae that are deposited on one host (Laval, 1972). This ensures that the larvae, which become adult without leaving their host, will obtain a sufficient supply of food to complete their development.

For *Vibilia armata* I found that there was usually a single larva per salp (Laval, 1963). This is true for the small salp species which are frequent in plankton samples of Villefranche *(Thalia democratica, Salpa fusiformis).* But Madin & Harbison (1977) rightly remarked that it is possible to find ten or more juveniles in a single salp, as illustrated by one of their photographs; in this case it can be seen that the salp was a large specimen. Thus for hyperiid species which exploit large hosts (relative to their size) the limitations are less stringent. This may be seen in the photographs given by Madin & Harbison (1977, Fig. 2: *Vibilia* sp. on a large solitary individual of the salp *Pegea socia*) or Harbison *et al.* (1978, Fig. 8: *Oxycephalus* sp. on the ctenophore *Cestum veneris).* In these photographs, the numerous juvenile amphipods are all clearly from the same brood. In samples taken by plankton nets, salp chains usually broke off. It is thus possible that the female *Vibilia,* for which the whole chain constitutes a single host, deposits her larvae at a single location and that, in small salp species, the larvae spread themselves on the chain, each (or a few) in the branchial cavity of a zooid. This would explain why in samples one larva is usually found per zooid.

Hyperparasitism is not infrequent, as is evident from the data given by Madin & Harbison (1977): 1200 juvenile *Parathemisto gaudichaudii* were found on a single chain of 13 salps, whereas the maximum egg number reported by Sheader (1977) for this species is 200. In *Hyperia spinigera,* the occurrence of individuals of very different sizes on the same host, the medusa *Periphylla periphylla,* was reported and interpreted as evidence of hyperparasitism by Thurston (1977). Hyperparasitism may also be deduced from the data of White & Bone (1972: Table I) on *Hyperia macrocephala* (mis-identified as *H. galba,* see Thurston, 1977) parasitizing the Scyphomedusa *Desmonema gaudichaudi.* Another example was given for *Hyperoche mediterranea* in the last section.

Both Metz (1967) and Thurston (1977) remarked that the number of juveniles on a single medusa is markedly less than the egg number of the hyperiid. Metz (1967) interpreted this difference as a loss, and attributed it either to predation on the juveniles by the host or to the escape of hyperiids after hatching. Thurston (1977) could not decide whether there was a loss of juveniles or if a single amphipod placed larvae on a number of medusae, obviously the correct hypothesis.

Thus even when the food supply is abundant, there is still a limitation, by the female herself, of the number of young deposited on a single host. This would have the advantage of 'not putting all her eggs in the one basket', *i.e.* to increase the probability of survival of the brood by spreading the risks between different individual hosts. This point is worthy of further research in the light of modern ecological theory.

LARVAL STAGES

Related to demarsupiation is the presence in many hyperiid species of a specialized hatching stage. This stage has all the characteristics of a larva, like the larvae found in other crustaceans. These characters are of two kinds: embryonic characters and specialized characters.

The hyperiid larva is a precocious stage in development. This is borne out by the incomplete segmentation and differentiation of the posterior part of the body: metasome and urosome. In some cases both the metasome and the urosome are embryonic; this stage was named pantochelis (Laval, 1965), the only appendages present being cheliform pereopods. In other cases, hatching occurs at a less precocious stage, the metasome being segmented and provided with imperfect (without setae and non-functional) pleopods; the urosome is undifferentiated. For these reasons this stage was called protopleon (Laval, 1965). When a pantochelis stage is present, it is followed through a metamorphosis (a major, non-gradual change in shape) by a protopleon stage. The protopleon phase (which may be composed of several, gradual stages) itself ends with a metamorphosis. This metamorphosis gives rise to the juvenile phase, where the young resembles a miniature adult, and corresponds to the hatching stage of gammarids. In addition to an

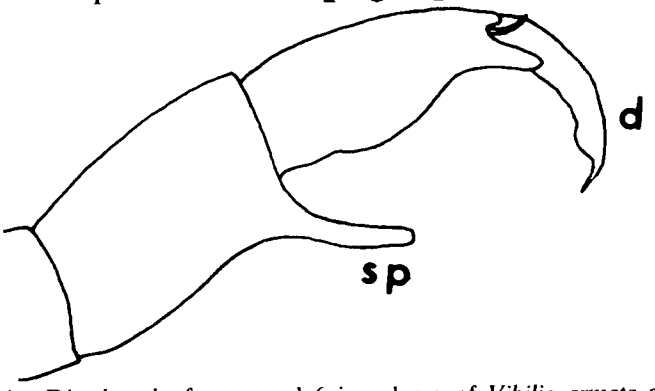


Fig. 4.—Distal end of pereopod 6 in a larva of *Vibilia armata* at the pantochelis stage: the carpus is produced in a styliform process (sp.), which will disappear at the next stage; note the hook at the tip of the dactyl (d) (from Laval, 1963).

incomplete abdomen the larval stages show embryonic eyes with no ommatidia. The larval habit, especially in the pantochelis stage, is very different from the juvenile appearance.

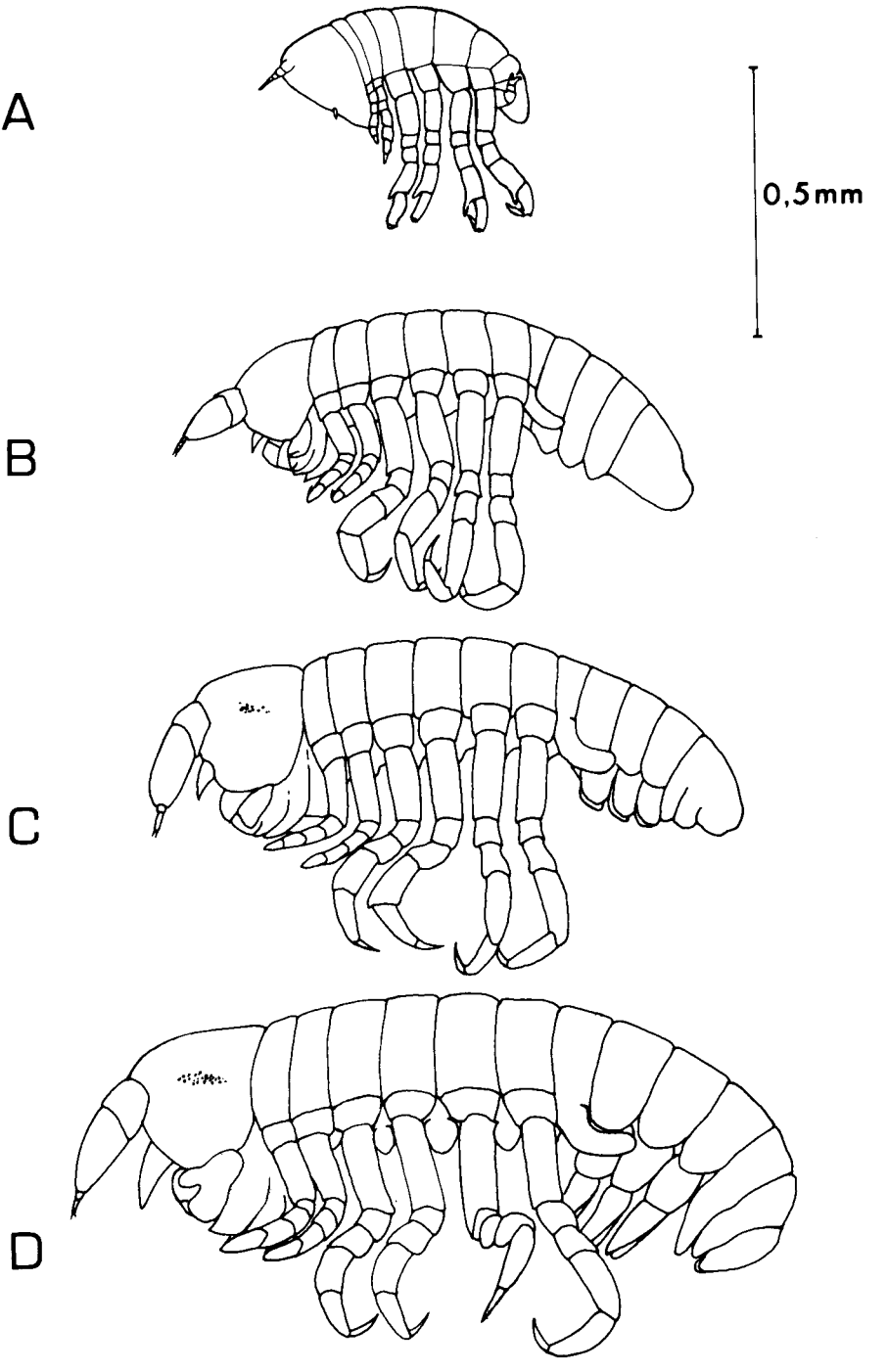
In addition to their embryonic characteristics, hyperiid larvae are provided with peculiar structures, clearly adapted to demarsupiation. They are essentially grasping differentiations, which will disappear after the first metamorphosis. A good example of such a formation is seen on the pereopods of the pantochelis larva of *Vibilia armata* (Fig. 4). Here the propodus (sixth joint) is produced in a long 'styliform process' (Laval, 1963), peculiar to the hatching stage, and the dactyl ends in a hooked, acute point; the two distal segments thus form a subchela, used to secure the larva to the host when it is transferred by the female.

Examples of larval developments

Larval developments of hyperiids are not known in great detail. The pantochelis stage of *V. armata* was illustrated by Laval (1963), but the protopleon phase of this species was only sketched in a subsequent note (Laval, 1965). Fig. 5 gives further illustrations of this two-phase larval development. The pantochelis larva of *V. armata* (Fig. 5A) changes into a protopleon I (Fig. 5B) after a moult, which is a metamorphosis. A remarkable fact is that the pereopods 7 have dedifferentiated, with no visible segmentation and only a subterminal seta. After the moult leading to the protopleon II, the major change concerns the metasome where bilobate protrusions represent the pleopods (Fig. 5C). At protopleon stage III the abdomen is not yet complete (Fig. 5D). The pleopods are represented by a peduncle with two unsegmented rami, which do not allow the animal to swim. The metamorphosis which ends the protopleon phase mainly concerns the abdomen. The one-podomere, non-functional pleopods change into 4-podomere, functional pleopods, while the urosome and uropods become fully differentiated (Fig. 5E). The podomere number is not always 4, it may range from 3 to 4½ (½ being incomplete segmentation).

We have seen previously that *Bougisia ornata* also hatches at a pantochelis stage, followed by three protopleon stages. The occurrence of a pantochelis stage in *Hyperoche mediterranea* was also mentioned; this stage is followed by three protopleon stages before giving a first stage juvenile (unpubl. obs.) No other pantochelis stages are known, with the exception of those of *Dairella latissima,* described by Stebbing (1888) under the name of *D. bovallii.* He found in this species a marsupial stage in which "no pleopods, uropods, or distinct telson, seem to be developed".

There are a number of hyperiid species hatching at a stage corresponding to the protopleon phase of *Vibilia.* There is only one protopleon stage in *Lestrigonus schizogeneios* (Laval, 1965, 1968a). In addition to the imperfect abdomen, this stage has all the pereonites free, while after the metamorphosis the five first pereonites are fused. In *Phronima sedentaria,* rearing experiments have shown three protopleon stages (Laval, 1975a). It should be noted that in this case a larval habit is retained in the last protopleon stage, despite the fact that pleopods and uropods are already fully segmented. The metamorphosis clearly occurs between stage III and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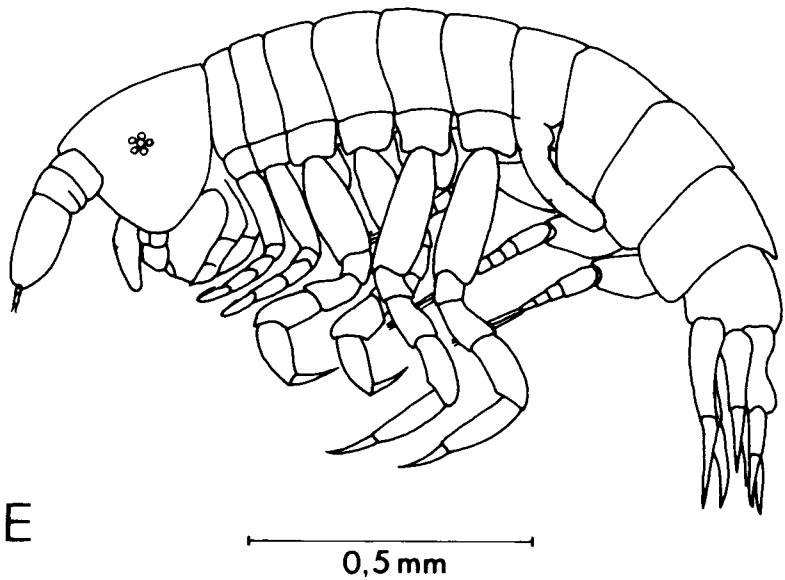

Fig. 5,—A–D, larval development of *Vibilia armata*: A, pantochelis stage (from Laval, 1963); B–D, protopleon stages I—III; E, first juvenile stage of *Vibilia armata*.

stage IV, only the latter displaying the 'specific form' (see the illustrations of Shih, 1969).

There are no other examples in the literature of larval development followed in the laboratory to the first juvenile stage. A few larvae belonging to the genus *Hyperia* are assignable or were assigned to protopleons. Bovallius (1889) and Hollowday (1946) described the larva of *H. medusarum*, which is similar to the protopleon larva of *Lestrigonus schizogeneios*. White & Bone (1972) sketched different instars of the protopleon larva of *Hyperia macrocephala*. These 'instars' could well be a unique stage, because it has been shown in the case of *Lestrigonus schizogeneios* (Laval, 1968a, p. 33) that the protopleon larva increases in size from 0·40 mm to 0·70 mm without moulting. Moreover the morphology of pleopods and uropods does not change during these 'instars'. Thurston (1977) also described a protopleon larva in *Hyperia spinigera*. In Villefranche, I found protopleon larvae in *Hyperietta stephenseni* (unpubl. obs.) and *Lycaeopsis themistoides* (Laval, 1965).

In the previous paragraphs, I intentionally omitted the case of the Platysceloidea. In Pronoidae, Lycaeidae, Oxycephalidae, Platyscelidae, and Parascelidae, the hatching stage does not resemble the adult; this is peculiarly striking in Oxycephalidae, but is also true in the other families. In most of the cases, however, all the appendages and segments are present at hatching and (except for the carpal process described by Bate, 1861, in the larva of *Brachyscelus)* no specialized structures are known (but the larvae are poorly described). In our present stage of knowledge, it is not possible to decide whether the changes from the hatching stage to the adult are gradual,

or whether the 'specific form' appears after a metamorphosis following the hatching stage. I provisionally propose to call the hatching stages of these families 'larvae', to emphasize that their appearance is distinct from that of the adult. That they are genuine larvae remains to be proved. These hatching stages were mentioned several times in the literature by Bate (1861): *Rhabdosoma whitei, Brachyscelus crusculum, Platyscelus serratulus*; Claus (1887): *Rhabdosoma armatum, Platyscelus ovoides, Parascelus* sp.; Stebbing (1888): *Calamorhyncus rigidus*; Bovallius (1890): *Rhabdosoma whitei*; Stephensen (1925): *R. brevicaudatum*; Brusca (1973): *Streetsia challengeri* (with a spurious supernumerary pereonite), *Rhabdosoma whitei*; Harbison (1976): *Lycaea pulex*; Harbison, Biggs & Madin (1977): *Eupronoe* sp. In Villefranche (unpubl. obs.), I also found such larvae in *Thamneus platyrrhyncus, Tetrathyrus forcipatus,* and *Amphithyrus sculpturatus.*

SIGNIFICANCE OF LARVAL DEVELOPMENT

The advantages of a precocious hatching, giving rise to a specialized stage are manifold and related to host infestation in the pelagic environment. Although deposition of young on hosts by the female is necessary, the egg number still needs to be as large as possible to counteract the scarcity and smallness of suitable biotopes (*i.e.* hosts) for the progeny. A parasitic benthic amphipod, living for example on hydroids, can move to another host if the first happens to perish. This is obviously not the case for the parasite of a pelagic host, which would be exposed to considerable hazards in looking for another one. In fact, the brood size of hyperiids such as *Hyperia galba* is bigger by an order of magnitude compared with gammarids (Metz, 1967). This increase in brood size is accomplished by a reduction in egg size, which is possible because development is not carried on to a functional, swimming stage. Furthermore, the increase in egg dimensions, which occurs at the end of incubation in gammarids (Sheader & Chia, 1970) and hyperiids lacking larval stages (Sheader, 1977), then occurs mainly when the larva is on the host (Laval, 1968a), thus avoiding a catastrophic loss from the marsupium. The host, continuing to protect the larva against predators and unfavourable environmental conditions may, therefore, be seen as a secondary brood pouch.

An indirect development also permits the larva to take advantage of embryonic potentialities. Crustacean larvae generally use these potentialities to adapt themselves temporarily to peculiar environmental conditions: consider for example the pelagic larvae of benthic decapods. Hyperiids also are thus adapted. Special grasping structures functioning in demarsupiation develop on the pereopods and later disappear. We have also seen the fully-segmented pereopods 7 of the pantochelis larva of *Vibilia* become de-differentiated and re-structured during subsequent stages. The rôle of pereopods 7 in the larva is not clear, but the fact that they are re-structured allows the formation of the special dactyl which will be used for demarsupiation by the adult.

Harbison (1976) was of the opinion that the morphology of the protopleon larva of *Lycaea pulex* does not necessarily indicate a parasitic existence, because he did not find this stage outside the marsupium. Presumably he did not find it because hyperiid larvae metamorphose quickly after feeding on

the host. In fact everything in the peculiar morphology and behaviour of hyperiid larvae implies a deposition on a host.

Some hyperiids do not hatch as larvae but, like gammarids, as juveniles. The only documented case is *Parathemisto gaudichaudii* (Kane, 1963a; Sheader, 1977). In Villefranche (unpubl. obs.) I found *Scina tullbergi* with juveniles in the marsupium, and I also observed that *Phrosina semilunata* carries juveniles, with functional pleopods, in the marsupium. It should be remarked that a direct development does not necessarily imply a free-living existence; we have seen that *Parathemisto* is associated with salps and medusae, *Scina* with siphonophores, and that the morphology of pereopods 7 in the Phrosinidae strongly suggests a rôle in demarsupiation. How then can these hyperiids with direct development succeed? From the above consideration of the advantages of larval stages, there may be two alternative explanations. First, for these species transfer and securing of the juveniles to the host could present no morphological problems. Secondly, if host specificity is not strict, juveniles could be demarsupiated rapidly when they begin to be active in the marsupium and yet with their low specificity not have difficulty in finding hosts; alternatively the specificity may be strict but the host very common and abundant. The former explanation may hold for *P. gaudichaudii*: rearing experiments have shown that "newly released juveniles tend to attach themselves and remain attached after feeding to any food source provided" (Sheader & Evans, 1975).

This raises the question of the hyperiid species found by Harbison *et al.* (1977) on 'marine snow', *i.e.* macroscopic non-living organic aggregates of sizes ranging from 1 mm to 30 cm. There is now accumulating evidence (Hamner *et al.*, 1975; Alldredge, 1976; Silver, Shanks & Trent, 1978) that this marine snow is of common occurrence in the pelagic environment. It is not known as yet whether marine snow is anything but an occasional resting place for hyperiids or if it constitutes a micro-habitat with species closely adapted to it. In the latter case one would hardly speak of parasitism; phoretism would not be adequate if the hyperiids feed on their support. This field is open for future research.

BEHAVIOUR OF LARVAE

The behaviour of *Lestrigonus schizogeneios* larvae was studied by Laval (1972). After demarsupiation, the larvae immediately eat the gonads or the manubrium contents of the host, the Leptomedusa *Phialidium*. Larvae experimentally placed on the subumbrella soon (in <1 h) gain a gonad or the manubrium, but they are in a less advantageous position than larvae deposited directly by the female inside these organs. It was demonstrated (by placing larvae on *Phialidium* with gonads and manubrium removed or on sections of pure umbrellar tissue) that the larvae require large quantities of umbrellar tissue to develop to stage II, greatly impairing the growth of the host, while larvae feeding on gonads or manubrium contents do little harm to the medusa; gonadal regeneration greatly exceeds removal by the minute larvae, and diversion of the food of the medusa has negligible effects at this stage.

Larvae of *Hyperia galba* rapidly spread into the gastrovascular system of the host, the Scyphomedusa *Aurelia aurita* (Metz, 1967), and the same

appears to be true of *Hyperia macrocephala* larvae on *Desmonema gaudichaudi* (White & Bone, 1972). For very young stages occupying this position, it was not possible for White & Bone, examining gut contents, to determine whether the amphipods were feeding on remains of prey caught by the host, on the host tissue itself or both. It should be noted that these medusae are much larger than *Phialidium*.

Vibilia larvae deposited on the surface of salps soon gain the inside of the branchial cavity and set up on the gill near the oesophagus (Laval, 1963). This observation was made on small salp species. For larger salps it is not known whether the female enters into the salp to demarsupiate the larvae, or whether the larvae themselves reach the branchial cavity. Larvae were seen grasping the wall of the branchial cavity with their gnathopods to bring it to their mouth (Laval, 1963). It has been shown by Madin (1974), however, that in the laboratory salps interrupt the secretion of the mucous web used to trap particles; it may be that the normal behaviour of *Vibilia* larvae is to feed on the food strand as do juveniles, in the way described and illustrated by Madin & Harbison (1977).

In *Hyperoche martinezii* (unpubl. obs.), the pantochelis larva digs its way into the mesogloea of the host (a ctenophore) as soon as it is demarsupiated. It does not burrow into the tissues with its mouthparts; it progresses backwards, the angle between the pereon and the folded rudimentary abdomen acting as a wedge. The backwards progression is effected by means of pereopods 3 to 7, sometimes aided by a pushing action of the gnathopods. The split tissues of the host apparently weld later.

In *Phronima* the larvae display a very peculiar behaviour. Soon after being demarsupiated, they grasp the barrel wall and arrange themselves in a compact cluster (Dudich, 1926). In the cluster the larvae (and later the juveniles) always show a spatial organization; whatever the cluster shape, the young are arranged in what Barnard (1932) called a "radiating manner", *i.e.* with the heads pointing outwards. Barnard's observation was made on a preserved sample, but I observed on live animals (unpubl. obs.) that, although the larvae are continually moving inside the cluster, they remain close together, keeping their orientation. When one larva goes a few steps in one direction, the nearest larva keeps close to it, and so do its neighbours. In this way the whole cluster slowly moves, and would eventually pass on to the outer barrel surface if the mother did not intervene. The indispensable rôle of the mother will be described later in this review. For the moment, it is sufficient to stress that the larvae display what Rabaud (1929) termed "interattraction", even when the mother is experimentally taken out of the barrel. When the larvae feed upon the prey brought back inside the barrel by the mother, they become agitated and lose their spatial organization somewhat; it is, however, recovered as soon as feeding ceases. Feeding of the larvae was described by Richter (1978), but he did not stress the importance of mutual attraction.

POSTURE AND LOCALIZATION ON THE HOST

Juvenile hyperiids are usually found in natural cavities of their hosts, or even, for some species, buried in the host tissues ("encysted juveniles" of Harbison *et al.*, 1977). The behaviour of *Hyperoche medusarum* and *H.*

mediterranea, digging a depression in the ctenophore surface, was reported by Flores & Brusca (1975). In *Lampetia pancerina* I observed juvenile *Hyperoche martinezii* progressing in a backward direction (like the larvae) in the mesogloea; juvenile *H. medusarum* were seen embedded in the mesogloea of the ctenophore *Pleurobrachia bachei* by Brusca (1970).

Most of the time juveniles and adult hyperiids adopt a 'resting posture' on their host; directed away from the host, the amphipod is attached by the dactyls of the last two or three pairs of pereopods, with only the dorsal surface of the pleon in contact with the host (Bowman, Meyers & Hicks, 1963; Laval, 1966, 1972; Evans & Sheader, 1972; Sheader & Evans, 1975; Westernhagen & Rosenthal, 1976; Madin & Harbison, 1977). Species of the genus *Vibilia,* lacking acute dactyls on pereopods 7, do not attach in a backward position. Juvenile *Platyscelus serratulus* have fully-segmented pereopods 7 (unpubl. obs.), which are used for attachment to the host, the siphonophore *Agalma elegans,* in a backward position. At a later stage, pereopods 7 regress, the distal segments and the dactyl degenerate, and attachment is effected by means of pereopods 3 and 4 only.

From time to time, the resting posture reverts to an 'active posture' ("forward position" of Sheader & Evans, 1975); the hyperiid swings down, facing the host, and moves to another place or feeds.

FEEDING

The feeding behaviour of hyperiids has only been investigated in a few cases. Such a study, in effect, requires rearing both the amphipod and its host; the behaviour of any hyperiid is not the same with and without the host. Field observations by divers are of the first importance to eliminate experimental bias, but they are necessarily short-term observations. There are also indirect ways of infering the feeding biology of hyperiids: morphological investigations on mouthparts and gut structure, and observation of stomach contents. We shall see that these studies may be seriously misleading.

The only quantitative laboratory study of an hyperiid associated with its host is the one of *Lestrigonus schizogeneios* with the Leptomedusa *Phialidium* (Laval, 1972). It could be taken as an example of an intimate association of an hyperiid with a host of small volume relative to its size. As they grow older, the juveniles of this species abandon the gonads. They feed upon the prey caught by the medusa, robbing the tentacles as soon as the prey is stung and brought back to the umbrella rim. The prey may also be eaten in the manubrium. When the young are small enough, they are frequently seen resting for days inside the manubrium (Fig. 6); they are not at all affected by the digestive enzymes, which nevertheless are harmful for crustaceans such as copepods. When the young are bigger, their size does not permit them to stay in the manubrium. They stay on the subumbrella, and go from time to time into the manubrium, stretching its lips with their gnathopods to feed upon its contents.

The effect of the hyperiid on its host was judged, in the case of *Lestrigonus schizogeneios,* by measuring the umbrella diameter of *Phialidium* with and without an amphipod (Laval, 1972). The harm to the medusa is roughly proportional to the size of the hyperiid. Negligible with the larvae, the effect on the growth of the host is not appreciable until the hyperiid reaches stage

VI (females are adult at stage VII, males at stage IX). This is only the consequence of the diversion of a part of the food of the medusa to the profit of the amphipod. When the medusa is not adequately fed or starved, the hyperiid finds its necessary requirements by eating the medusa itself. The host is then devoured before the hyperiid becomes adult, while with a normal food supply the hyperiid can reach adult or subadult condition on the host on which it was initially deposited by the female. The host is nevertheless eventually consumed by the amphipod.

The behaviour of *Lestrigonus schizogeneios* juveniles, diverting the food from their host, is also found in other species. Juveniles of *Bougisia ornata* display the same behaviour as *Lestrigonus schizogeneios* (Laval, 1966). In *Vibilia* species, juveniles placed near the opening of the salp's oesophagus take parts of the food-strand of the host with their gnathopods for their own nutrition (Madin & Harbison, 1977). If the normal feeding mechanism of the salp—trapping particles in a mucous filter net (Madin, 1974)—is interrupted, as is the case when salps are kept in the laboratory, the *Vibilia* feed upon the host.

Large hosts are probably capable of being eaten by hyperiids of small size relative to their own size, and balance this consumption by growth and regeneration. It is difficult to be certain that in laboratory conditions hosts are adequately fed, and that host consumption represents normal behaviour. There are, however, some observations and indirect evidence suggesting that diversion of the food of the host and host consumption occur together in some cases. Thus, Sheader (1973) observed that *Hyperia galba* maintained in the laboratory fed both on the tissues of the host (Scyphomedusae) and on prey captured by the host. Dahl (1959a, b) found nematocysts of the host, with some remains of host tissue, in the digestive tract of this species, and Metz (1967) found evidence of destruction of gonads; he noted, however, that eating of the gonads was mostly due to older *Hyperia* and that young were burrowed in the gelatinous tissues of the medusae or found in the radiary canals. These two observations were discussed by Laval (1972), who stressed the fact that all Scyphomedusae are plankton-feeders, which concentrate planktonic prey, agglutinated in mucous strands, in 'food pouches' before transferring them to the manubrium. *H. galba* is actually mainly found in these food pouches (Hollowday, 1946). Laval (1972) concluded that *H. galba* must feed mainly on this rich food, but could feed from time to time or when the medusa has insufficient food, on the host itself. Thurston (1977), studying a related species, *H. spinigera,* also associated with Scyphomedusae, found nematocysts and material containing protoporphyrin likely to come from the host in gut contents of the hyperiid. He could not rule out, however, the possibility that this species, and particularly the smaller juveniles, feed on the food of the host, rather than on the medusa itself. White & Bone (1972) could also not determine, from examination of gut contents, whether juvenile stages of *H. macrocephala* (another *Hyperia* associated with Scyphomedusae) were feeding on material found in the digestive system of the host or the host's tissues, or both.

For a few species, for which we have some observations, it is not clear whether juveniles feed only upon the host's food. *Lycaeopsis themistoides* occupies the anterior nectophore of diphyid siphonophores. Harbison *et al.* (1977) found this species in U-shaped burrows dug in the anterior

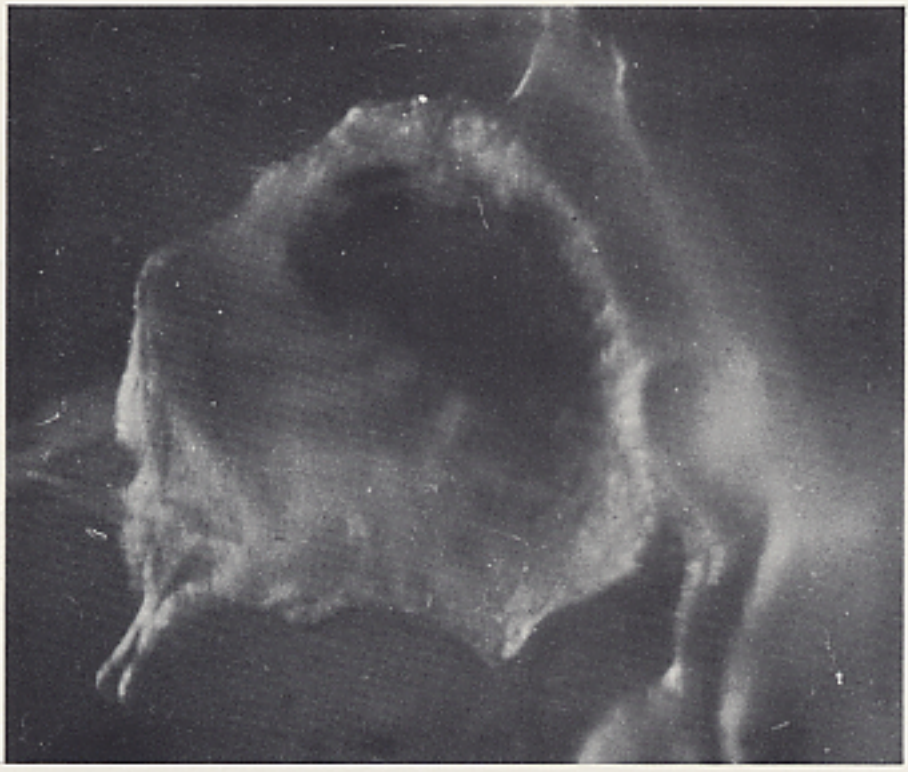

Fig. 6.—A juvenile *Lestrigonus schizogeneios* staying in the manubrium of its host, the Leptomedusa *Phialidium* sp.: the juvenile is unaffected by the digestive enzymes and may be seen by transparency eating a metanauplius of *Artemia salina*.

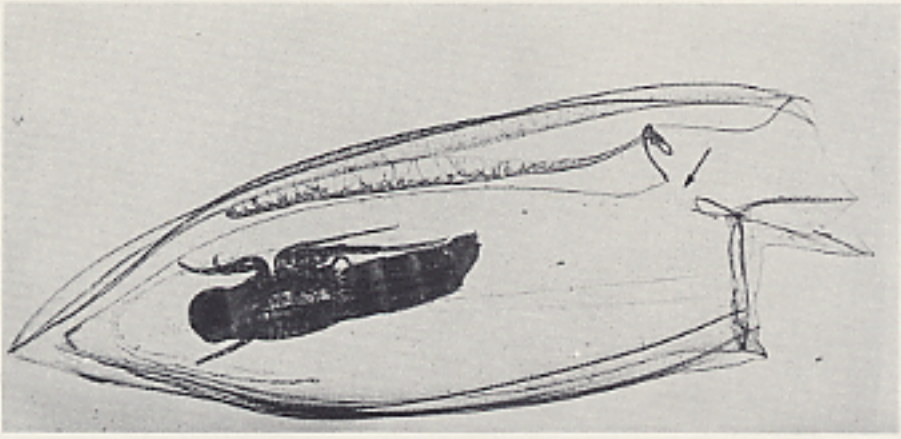

Fig. 7.—*Lycaeopsis themistoides*, subadult male in the anterior nectophore of the siphonophore *Chelophyes appendiculata*: the hyperiid has dug an opening (arrow) by which it can reach the stolon; siphonophore length is 14 mm.

[*To face page 38*]

nectophore of *Diphyes dispar*; on one occasion the distal part of the somatocyst was entirely eaten and, as this observation was made by divers, it is proof that the host may be eaten in the field. I made additional (unpubl.) observations on this species, which is found in Villefranche in *Chelophyes appendiculata*. The juvenile digs an excavation near the opening of the nectophore, just below the hydroecia, and eventually pierces a hole which makes a communication between the cavity in the nectophore and the hydroecia (Fig. 7). Through this opening, it can reach the stolon. It is unclear whether the hyperiid uses this access to eat the prey caught by the siphonophore or to eat the zooids (the siphonophore was not correctly fed in the laboratory). Juveniles of *Lycaeopsis themistoides* also eat the epidermis which lines the inside of the nectophore; they may be observed digging small pits with the mouthparts, the bent antennae 2 tapping rapidly against the wall. The epidermis of the living siphonophore can be vitally stained with neutral red; the colour may be seen to pass quickly into the hepato-pancreatic caeca. In Lycaeopsidae (as well as in Platyscelidae and Parascelidae) there are reduced mouthparts, which are perhaps used for piercing and sucking the liquid contents of radiary canals and gastrozooids of siphonophores.

Individuals of *Hyperoche* living on ctenophores were observed on the host's surface or imbedded in the mesogloea (Brusca, 1970; Evans & Sheader, 1972; Flores & Brusca, 1975). No evidence of permanent damage was present. It may well be, in this case as in other similar cases, that the gelatinous tissues of ctenophores are of a much lower nutritive value than prey such as copepods, and thus that the latter are preferentially consumed by the hyperiid. There are, however, species of *Hyperoche* found on *Beroe forskali* (see Tables I and II), a ctenophore which, like *B. ovata* (Swanberg, 1974), feeds on other ctenophores.

Finally, some hyperiids appear to feed directly on the host's tissues. Individuals of the genus *Lycaea* found on salps do not feed on the mucous food strand as do *Vibilia,* but were seen *in situ* by divers grazing on cilia rows of the gill bar, or consuming developing embryos of the host (Madin & Harbison, 1977). In Villefranche, *Lycaea pulex* is also observed in pyrosomes. Very young individuals may be found in the branchial cavity of zooids, while more advanced stages occupy the locations of eaten zooids (unpubl. obs.). Obviously *Lycaea* does not divert the host's food but devours the host itself. Observations of Harbison *et al.* (1977) and personal observations strongly suggest that *Brachyscelus* behaves like *Lycaea.*

With the diversity of hosts which was depicted at the beginning of this review, it is not surprising that different methods of feeding are found among hyperiids. These methods depend on the particular morphology and biology of the host, the relative sizes of both partners, and the intimacy of the relationship.

THE PREDATORY BEHAVIOUR OF ADULT HYPERIIDS

Whether the host is deprived of an increasing fraction of its food or progressively eaten by the juvenile there is, in any case, a balance between hyperiid depredations and regeneration or growth of the host. This is clear in the quantitative study of *Lestrigonus schizogeneios* (Laval, 1972). The point

when the balance becomes negative for the host depends on a number of factors: the relative sizes of both partners and the developmental stage of the hyperiid, the number of hyperiids per host, the host's capacities for regeneration and growth, the nutritive value of the host's tissues or the amount of food captured by the host. Cases are conceivable of hosts large enough, living in a rich food environment, for which the association does not reach a fatal state. Such hosts would be able to support the entire development of the hyperiid without being killed, and perhaps even another generation. This could probably occur with large Scyphomedusae and *Hyperia*. Such cases would, however, be the exception rather than the rule; considering the size range of adult hyperiids and their potential hosts, it may be predicted that usually the host will be devoured towards the adult stage of the hyperiid. Some adult hyperiids are known, from laboratory or field observations, to be able to devour zooplankton in a very short time: *Parathemisto gaudichaudii* (Williamson, 1949; Kane, 1963b; Sheader & Evans, 1975); *Phronima curvipes* (Laval, 1968b); *P. sedentaria* (Richter, 1978); *Lestrigonus schizogeneios* (Laval, 1972); *Vibilia armata* (Laval, 1974a); *Hyperoche medusarum* (Westernhagen & Rosenthal, 1976); *Oxycephalus clausi* (Harbison *et al.*, 1977, 1978). This is probably true for the majority of hyperiids when they become large enough to kill their hosts.

In my opinion when considering hyperiids 'predator' should not be taken as meaning 'totally free-living'. I do not think that most adult hyperiids, with their gammarid-like morphology, are able to maintain a wholly pelagic existence. They would rather wander from host to host. By 'host' I mean gelatinous zooplankton, used as a resting place as well as source of food, and perhaps also as a platform for attacking prey. This conception could be extended to the 'marine snow', consisting of remains of gelatinous hosts, egg masses or even mucous secretions. Hyperiids were found *in situ* on these supports by Harbison *et al.* (1977).

Hyperoche medusarum was considered free-living at all developmental stages by Westernhagen (1976), Westernhagen & Rosenthal (1976), and Westernhagen, Rosenthal, Kerr & Fürstenberg (1979). This is probably a misconception, deduced from the fact that young and adult individuals were collected free-swimming when attracted by a powerful light. Harbison *et al.* (1977) observed underwater that electric light induces a "frenzied swarming" of hyperiids, and further suggested that "white light induces behavioural modifications, perhaps causing the amphipods to quit their hosts". Evidence presented above shows that *H. medusarum* is indeed associated with medusae and ctenophores during at least larval and juvenile stages. This species is probably a predator (in the above sense) only when adult.

The laboratory conditions in the experiments of Westernhagen & Rosenthal (1976) and Westernhagen *et al.* (1979) did not resemble natural conditions. Any hyperiid immersed in a beaker overcrowded with edible animals would grasp them. Furthermore, in these studies "wounded", "dead" and "partially eaten" fish larvae were pooled in the same category as "completely eaten" larvae; only this category corresponds to true predation. Experiments conducted with a prey density ten times higher than the density in the natural habitat gave a maximum rate of "attack" (which is probably an over-estimation of true predation) of about 0·7 fish larva per h.

Corrected for crowding and false attacks, this seems rather inefficient. Eating slowly-swimming medusae, with highly nutritive manubrium contents or gonads, would be less energy-consuming for the hyperiid.

Hyperiids of the genus *Parathemisto* were also considered free-living and treated as such for feeding experiments (Kane, 1963b; Sheader & Evans, 1975). *P. gaudichaudii* was recently shown to be associated with salps (Madin & Harbison, 1977). Association of newly released juveniles with Hydromedusae was already apparent from a study by Sheader & Evans (1975). These authors remarked that when food sources such as living Hydromedusae were used, "the juveniles become and remain attached, resulting in a high rate of survival". This study is also particularly interesting because "conditioning" of food was shown in *P. gaudichaudii*: "observations and results suggested that a prey species was more likely to be taken as food if it had previously formed the diet of *Parathemisto*". Thus, juveniles deposited on a host by the female could select preferentially individuals of the same species or related species as food. Raptorial behaviour is well established in this genus (Kane, 1963b; Nemoto & Yoo, 1970; Sheader & Evans, 1975). Evans & Sheader (1972) suggested that large prey, such as Hydromedusae or the euphausiid *Meganyctiphanes norvegica,* provide a means of transport after the *Parathemisto* has fed. The few reports on the respiratory rates of hyperiids (Conover, 1960; Childress, 1971; King & Packard, 1975; MacDonald & Teal, 1975; Ikeda, 1976, 1977a, b) have never taken into account the fact that metabolic needs in natural conditions could be less when the hyperiid is attached to a living support. The respiratory rate of *Phronima sedentaria* was measured in its barrel by Mayzaud & Dallot (1973). This species represents a special case raising methodological problems.

Thus, when the hyperiids attain a size large enough to devour their hosts, they probably adopt a predatory behaviour. Their prey would be mostly slow-swimming gelatinous zooplankton, on which they were 'conditioned' during their early existence. The Lanceolidae or the Platyscelidae, which do not have the morphology of good swimmers, probably go from one gelatinous animal to another, the prey being used as a resting place. Others, like the Phrosinidae, well-adapted to a pelagic life, are likely to prey on concentrations of zooplankton. *Parathemisto* would be between these two extremes.

GUT STRUCTURE AND FOOD

There are a number of reports on the anatomy and histology of the digestive tract of hyperiids: Claus (1879, 1887), Garbowski (1896), Vester (1900), Funke (1912), Woltereck (1927), Dunbar (1946), Bowman (1960), Agrawal (1967), Evans & Sheader (1972), Sheader & Evans (1975). So far these investigations have not lead to firm conclusions on feeding habits. Evans & Sheader (1972) found, for example, that the gut of *Hyperoche medusarum* was far simpler than that of *Hyperia galba,* studied by Agrawal (1967); according to Evans & Sheader (1972), this would reflect differences of diet. *H. galba* would feed on the prey caught by its host, while *Hyperoche medusarum,* the gut of which was only filled with an unidentifiable substance, would only eat soft food, presumably ctenophore tissues from its

host. Westernhagen (1976), however, found crustacean remains in the gut contents of *H. medusarum*, and also showed that laboratory specimens dissected shortly after being fed on live herring larvae had gut contents composed of the same unidentifiable mush as the field specimens. Thus, at least in this case, the anatomy of the digestive tract seems a poor indicator of possible diet. Such questions could perhaps be better answered by enzymological investigations, which have not yet been done on hyperiids.

By themselves, stomach content studies do not distinguish between food ingested directly by the hyperiid from that first caught by the host. Moreover the small number of identifiable items may be misleading; for example, an hyperiid having a diet of, say 95% salp and ctenophore tissues and 5% crustaceans will have stomach contents composed of crustacean remains in an unidentifiable substance, along with a little phytoplankton coming from the salps' guts. Undischarged nematocysts are frequent in gut contents or faecal pellets of many hyperiids (Woltereck, 1927; Vinogradov, 1957; Dahl, 1959a,b; Repelin, 1970, 1978; Legand *et al.*, 1972; White & Bone, 1972; Laval, 1974b; Sheader & Evans, 1975; Zhuravlev & Neyman, 1976; Thurston, 1977; Richter, 1978). They may originate from the host (but this would be difficult to prove, see Thurston, 1977) or from cnidarian prey, or even from cnidarivorous prey. In any case because they are undigested and conspicuous, their number may lead to an over-estimation of the amount of ingested cnidarians relative to other gelatinous zooplankton.

These uncertainties are the consequence of our ignorance of hyperiid behaviour. Although in fish studies stomach contents and gut structure can give useful indication of the diet, crude attempts to apply the same methods on hyperiids are likely to produce biased results. The deductive process should rather be inverted; that is, if the behaviour is known, stomach contents and gut structure could give quantitative precisions on such matters as food specialization, niche structure or energy flow in pelagic ecosystems.

MATING

Mating in hyperiids has so far only been observed in *Parathemisto gaudichaudii* (Sheader, 1977). A site of attachment was found to be necessary for successful mating, which occurred in the laboratory on the host (Hydromedusae) or occasionally on pieces of food provided for the amphipod. There was no long precopulation stage as in gammarids. This is probably the case for all hyperiids: there are no reports of precopulation in the literature, and over many years of observation of live hyperiids I have never seen it. In *Parathemisto* copulation occurred, as in gammarids, just after moulting of the female, when the oostegites are not fully extended, leaving an opening by which the male transferred a sperm bundle into the marsupium. The excavate organ described by Kane (1963a) was used for handling the sperm bundle. The excavate organ is found on uropods 1 of most Hyperiidae, but not in other families.

In aquatic gammarids, the long precopulation period before the moult of the female ensures that a male will be available during the short time following the moult and preceding the hardening of the cuticle. In hyperiids there is no necessity for the male to attach to the female if both partners are

attached to a host. In *Parathemisto gaudichaudii,* the male plays its antennal flagellae over the body of the female (Sheader, 1977) probably to get chemical information on its sexual and moulting states. Such body-touching by the antennae was also observed in terrestrial talitrids (Charniaux-Cotton, 1957), in which there is no precopulation before moulting of the female. Another point in which hyperiids are similar to talitrids is the rapid hardening of the dactyls after moulting. In talitrids this is an adaptation to terrestrial life (Charniaux-Legrand, 1952). In hyperiids moulting occurs on a pelagic host, and the freshly moulted animal must secure a grip on the host with the dactyls as soon as the old cuticle is abandoned (Laval, 1972).

If females eventually consume their hosts at the end of their development, they must find a new one for mating. They probably stay on this host during the incubation of the eggs and leave it after demarsupiation of the larvae. Other hosts will then be sought for disseminating the remaining larvae. Thus, adult females would be associated with hosts most of the time, whereas adult males would be mostly free-swimming predators. This is also strongly suggested by SCUBA observations and morphological considerations (Harbison *et al.*, 1977).

SEX RATIOS IN PLANKTON SAMPLES

Tertiary sex ratios (*i.e.* that of the reproductive population) differing from the 1:1 equilibrium have frequently been reported for hyperiids (see, *e.g.* Stephensen, 1925). These data should, however, be considered with extreme care as sampling methods by themselves may lead to biased sex ratios, because of the different behaviour of males and females in relation to hosts.

In *Vibilia armata,* the adult sex ratio in plankton samples was found to vary according to the diameter of the net (Laval, 1974a); small nets caught almost only females, while large nets caught nearly equal numbers of both sexes. Counts of males and females from 1570 samples plotted against net diameters showed a curvilinear relationship, with an asymptote towards equilibrium at large diameters. A mathematical model was developed to explain this curve, on the assumption that adult males are free-living or not tightly associated with hosts, and thus able to avoid small nets, whereas females closely associated with salps do not react to the approaching net. The fit with the model predictions was satisfactory, when taking into account certain necessary approximations. A better fit was obtained if one assumed that a small proportion (<30%) of females was not associated with hosts. As a practical result it was found that at least a 6-foot Isaacs–Kidd midwater trawl towed at 3 knots is required to catch a representative number of *V. armata* males. Differential avoidance of approaching nets between males and females is likely to occur for most large (*i.e.* >5 mm) hyperiid species, and the importance of this has not yet been realized (*e.g.* by Shulenberger, 1977). Unfortunately this is not the only methodological reason for erroneous tertiary sex ratios.

In *Phronima sedentaria* females largely outnumber males in plankton samples (Stephensen, 1924; Brusca, 1967; Repelin, 1970). Counts of stage IV juveniles caught in the mother's barrel show that the secondary sex ratio (*i.e.* that at hatching) is not significantly different from 1:1 (unpubl. obs.).

But differential avoidance is not the only source of error, because in this species males are very much smaller than females and thus are more likely to escape through the meshes. Such a source of loss has indeed been demonstrated in this species by Repelin (1978). Nevertheless the possibility of a biased tertiary sex ratio in *P. sedentaria* is a real one; for example large females could be more conspicuous than males to predators. This phenomenon will, however, be obscured in samples by the combination of differential avoidance and escapement through the meshes, and thus very difficult to demonstrate.

In some hyperiids males are unknown. This may be due to taxonomic confusion. Oxycephalids of the genus *Rhabdosoma* present a more intriguing problem. The species of the "second group" *(R. brevicaudatum* and *R. minor)* were thought by Fage (1960) to be parthenogenetic. In *R. brevicaudatum,* only two young males were found by Stephensen (1925) and Fage himself (1960) out of the 855 specimens reported in the literature up to 1959. The few specimens reported since 1960 up to now for which a sex determination was given were also females (Hoenigman, 1963: five females; Shulenberger, 1977: one female). In *R. minor* no males have ever been reported, where 1921 females were caught on the Dana Expedition (Fage, 1960); to this number one can only add one female reported by Brusca (1973). As a further argument for parthenogenesis, Fage (1960) added that eggs in early stages of development were found in the marsupium of *R. brevicaudatum* together with late embryos; if a fecundation had taken place, the embryos would all have been at the same stage. Before confirming the occurrence of parthenogenesis in these species, however, it will be necessary to do rearing experiments. Sampling bias cannot totally be ruled out; the small *Rhabdosoma* of the second group are slender enough for the males to pass actively through the meshes when caught, while the females would stay on their hosts (presumably ctenophores destroyed by the catching process).

Swarms composed of individuals of only one sex may also upset the sex ratio in plankton samples. Only species of the genus *Parathemisto* appear to make bisexual swarms at the time of reproduction (Le Danois, 1921; Nemoto, 1959; Gray & McHardy, 1967). Swarming in this genus has not been reported with certainty from visual observations at the sea surface, but is attested by accumulation of stranded specimens (Norman, 1900; Tesch, 1911; Wiman, 1943; Gray & McHardy, 1967), and underwater observation (Fenwick, 1978). Unisexual catches entirely, or almost entirely, composed of adult males on the surface at night correspond to another form of behaviour. These catches have been reported for *Hyperietta vosseleri* (Barnard, 1930, as *Hyperia fabrei*); *Platyscelus serratulus* (Pirlot, 1930; Fage, 1933); *Hyperietta luzoni, Eupronoe armata, Paratyphis maculatus* (Pirlot, 1939a); *Hyperioides sibaginis* (Nair, 1972); *Phrosina semilunata* (Merrett & Roe, 1974); *Anchylomera blossevillei* (Shulenberger, 1977). A number of these captures were made under a light with a hand net, but others were made using plankton nets. Swarms of male *Hyperioides sibaginis* over a distance of 12 nautical miles were reported by Nair (1972). Pirlot (1939b) advanced the hypothesis that, like the gammarids studied by Fage (1933), hyperiids have a nocturnal pelagic phase during which they leave their hosts and wander in the plankton. It is now known that the behaviour reported by Fage (1933) was due to the attraction of electric light.

Nocturnal plankton collections of gammarids, made without light, give various results; during the night there is in many gammarids an increase in activity which may be limited to one sex or to juveniles, depending on the species, the time of night, the time of year, *etc.* (Macquart–Moulin, 1968, 1971, 1976). The adult males of hyperiids which are, as we have seen, probably free-living, may concentrate at the sea surface during moonlight. Full moon was not recorded in Nair's report (1972) but probably occurred, as at the time of the swarm (which was maximum between 01.00 and 02.00 h) flying fishes and sharks were observed from the ship.

Shulenberger (1977) found, in repeated 5-min tows made with a neuston net during one night, either only adult males or only adult females of *Anchylomera blossevillei.* Unfortunately the numbers of individuals caught in each tow were not given, so that it is impossible to know if female catches were as important as male catches (numbers per tow were only said to range from <10 to >1000). If not, a simple explanation could be that if concentrations of males occurred under the influence of the moon in some places, in adjacent places the net would catch only scattered females.

MIMICRY

The transparent, balloon-like females of the genus *Mimonectes* were said by Bovallius (1889) to mimic pelagic plankton, but this was questioned by Woltereck (1904b). It is an observational fact that some hyperiids mimic, by their colour and sometimes also by their overall shape, a part or an organ, of their host. Adult *Vibilia viatrix,* which are generally positioned at the oesophagus of salps of the genus *Pegea,* closely match in colour the salp's nucleus (Madin & Harbison, 1977). The same thing is observed in *Vibilia jeangerardi* associated with *Salpa maxima* (unpubl. obs.). The coloration of *Brachyscelus rapacoides* is very similar to that of the hydromedusa *Leuckartiara* sp. on which it is found (Harbison *et al.,* 1977). The chromatophores of *Lycaea pulex* found in *Pyrosoma atlanticum* have exactly the colour of the spots which are on the gut of the tunicate zooids; juveniles and adults of *Platyscelus serratulus* are perfectly hidden between the zooids of the siphonophore *Agalma elegans,* which has the same colour and, moreover, the globular juveniles mimic the tentillae of the gastrozooids. Juvenile *Thyropus typhoides* show the same pigmentation as the *Forskalia* species on which they are attached (unpubl. obs.). A related species, *Thyropus similis,* is colourless but resembles a palpon or a gastrozooid of its host, the siphonophore *Athorybia lucida* (Biggs, 1978).

The adaptive value of this mimics remains to be proved. It seems likely that, being invisible on the host, the hyperiids would escape the attention of predators such as fishes.

IMMUNITY

Immunity to nematocyst discharges is obviously required for hyperiids associated with cnidarians. This is easily verified by laboratory observations. This immunity is often supplemented by an invulnerability to digestive enzymes: for instance it has been mentioned above that several Hyperiidae live, during larval or juvenile stages, in the gastrovascular system of medusae.

The presence of an hyperiid inside the gastrovascular cavity of a cnidarian does not imply that the hyperiid was preyed upon. Biggs & Harbison (1976), speaking of *Schizoscelus ornatus,* stated "if the amphipod's freedom of movement is restricted, as when it is enclosed in a jar with its host, it can be captured and quickly ingested". It is not clear whether in this case ingestion was followed by digestion. Harbison *et al.* (1977) also found a specimen of *Hemityphis rapax* inside a gastrozooid of a colony of *Forskalia tholoides* "not appreciably digested", and the context indicates that the authors considered it a prey rather than a parasite.

There are no studies on the mechanisms by which an hyperiid can resist the stings of nematocysts, and digestive enzymes, which are fatal to other crustaceans. There are, however, some studies on gammarids which may shed light on this question. Comparison between free-living gammarids and gammarids living in the gastrovascular cavity of sea anemones led Vader & Lönning (1973) to propose that tolerance to toxic substances (probably proteolytic enzymes) emitted by the host is genetically determined and not acquired during the life of the amphipod. In *Melita obtusata,* which lives on *Anemonia sulcata,* contact with the tentacles elicits a nematocyst discharge, which does not harm the amphipod, but the feeding response of the anemone is inhibited (Hartnoll, 1971). On the other hand, immunity against nematocysts is possibly only a property of the cuticle. The waxes responsible for the hydrophobous character of the cuticle (a character present in all hyperiids) are perhaps related to this inhibition. Obviously more experimental work on this question is needed. Inhibition of nematocyst discharge in the digestive tract is easier to explain, as most viscous or enzymatic secretions prevent this discharge (Salvini–Plawen, 1972); this mechanism is thus not highly specific.

MATERNAL CARE AND SOCIAL ORGANIZATION: THE CASE OF PHRONIMIDS

In the section on larval behaviour, the occurrence of an "interattraction" bringing larvae and juvenile phronimids in close contact was mentioned. Some unpublished observations may help to understand this behaviour. In the barrel, the spatial organization of the young is kept even when the experimenter removes the mother, but this action soon has fatal consequences for the brood. When the mother is missing, the whole group of larvae, in its continuous movement, sooner or later reaches one end of the barrel and passes on to the outer surface. In this exterior situation, the young cannot be fed by the mother, which brings back the prey to the inside of the barrel. Passage of the young on to the outer surface is, however, prevented by the female. By 'combing' the young inwards with the tip of the gnathopods, she forces them back in the middle of the barrel. Combing of the young is facilitated by the presence of two wing-like plates—the dactyloptera of Bate (1862)—on the tip of the gnathopods. Alternating the direction of combing (by the somersault movement described by Minkiewicz, 1909) causes the young to be concentrated in the middle part of the barrel. In this way they cannot pass to the outside, where they would be lost. This would not be possible in the absence of interattraction, which allows the group to be manipulated as a whole. The rôle of the female is thus two-fold;

she brings prey to the brood and she prevents it from passing on to the outer barrel surface.

Among insects there are well-known examples of 'maternal societies' in which the mother lives with her brood. These societies range from very simple ones, as in mole-crikets *(Gryllotalpa)* and earwigs *(Forficula, Labidura)* where the relationships of mother and brood are rudimentary, to complex ones, as in social wasps and bees where the progeny stay with the mother once adult. In all these maternal societies a nest is made, and the young are kept together by interattraction. To my knowledge, phronimids are the only crustaceans showing maternal societies. Like primitive social insects, such as wasps of the genus *Belonogaster,* the mother stays with the larvae (and phronimid larvae display an even greater spatial cohesion than does *Belonogaster*); like eumenid Hymenoptera, which show only tendencies towards social life (Roubaud, 1916), the mother feeds her larvae by bringing them prey. In contrast to eumenids and social wasps, however, phronimids make a nest from a living host, an habit closer to that of parasitoid insects which lay their eggs on or inside a host.

From an ecological point of view, the advantages of maternal societies are obvious. In *Phronima sedentaria,* there are up to 600 young at stages I or II in the barrel. For the young, until they leave the barrel, there is no energy cost to find food, and no risk of being eaten by a predator (except for the collective risk involving the whole barrel). For the female, there is no energy wasted in seeking numerous hosts once the barrel is made; moreover, this social behaviour allows her to have more offspring than if she had to find a host for each larva. The same result could not be achieved by depositing the whole brood on a single host, because this host would quickly be devoured. In addition, the barrel is passive, and the female, with her powerful swimming ability, can drive it to favourable feeding places.

This extraordinary (for a crustacean) maternal society has not yet been studied in detail, and many questions are still unanswered (for example, why does the mother not eat the young when they moult?). Insight from works on insect societies will certainly prove useful, but future research will perhaps reveal features specific to the pelagic environment.

THE NATURE OF THE RELATIONSHIP: HYPERIIDS AS PARASITOIDS

In the preceding pages several examples of relationships of hyperiids with zooplankton have been reviewed; some general characteristics may now be stressed. All hyperiids are associated with gelatinous zooplankton at the onset of their existence. This 'symbiosis' (in a broad sense) is, depending on the hyperiid species, more or less intimate, and its duration varies according to biological and ecological factors. Nevertheless the relationship is nearly always detrimental to the host, which is usually devoured only when the hyperiid reaches the adult condition.

Rather than 'protelean parasites' (*i.e.* animals parasitic only in their young stages), the word 'parasitoid' in my opinion better qualifies the majority of hyperiids. It has been chiefly employed for insects, but it applies fairly well to hyperiids, as shown by the two (among many others) following quotations. According to Askew (1971), "a parasitoid at first feeds like a parasite, being adapted to living in intimate physical association with its

host, and only after it has extracted all the nourishment that it requires from the host's living body does it eventually destroy the host". For Knutson & Berg (1966), the word parasitoid is an "adjective (. . .) characterizing a range of feeding behaviour intermediate between the parasite and predaceous ends of the behavioural continuum".

The latter definition, referring to a continuum, is preferable to rigid ones setting marked boundaries between commensalism, parasitism, and predation, which certainly do not exist and are likely to lead to sterile word battles. Of course some examples may be found where the hyperiids are more or less typical parasitoids. Hyperiids of the genus *Parathemisto* appear to leave their host at an early stage, and from then on to behave more like predators, with prey used as resting places. In other cases, the living host is perhaps replaced by an organic substratum (marine snow or mucous secretions originating from macroplankton); it is not known, however, if this is a normal, durable and viable behaviour. There are also some borderline cases, such as *Phronima* digging barrels in tunicates. Except for these extreme cases, most hyperiids fit the definition well with some, such as *Bougisia* laying its eggs in the host's tissues, being strictly equivalent to insect parasitoids. Hyperiids are indeed amphipod parasitoids. To treat them as free-living crustaceans would expose the researcher to serious mis-understandings. This may be seen in several ecological and oceanographical studies, even in recent ones, and will now be discussed.

SOME OCEANOGRAPHICAL PROBLEMS

QUANTITATIVE ESTIMATES OF HYPERIIDS

In addition to the classical difficulties encountered when sampling zooplankton, quantitative sampling of hyperiids presents special problems. Some of them, such as differential avoidance between sexes and swarming of males, have already been touched upon in the preceding pages. There is a more general difficulty related to the parasitoid habits of hyperiids; being parasitic, they amount to only fractions of their host populations. This means that they usually are rare zooplankon, except for a few occasional (behavioural) concentrations. This is acknowledged by Thurston (1976) when he states that (pelagic) "amphipods frequently form but a small part of the zooplankton biomass". Moreover, being on hosts which are likely to occur in patchy distributions, such as salps or medusae, they are not randomly distributed. Most of the time they are caught by chance, *i.e.* individuals would not necessarily be present in replicated tows. Unfortunately, plankton samples are not often replicated (and this may be not feasible with deep tows); the necessity of replicates was stressed by Shulenberger (1978). Counts from unreplicated samples are not representative of real abundances. To get workable numbers, very long tows would be necessary, with the obvious inconvenience of mixing different layers, stations or periods of time, and eventually zooplankton communities. The result is that up to now distributional studies on hyperiids are generally unreliable (see Shulenberger, 1978).

Once hyperiids are properly understood as parasitoids, however, these

sampling problems become of secondary importance. Hyperiids viewed as parasitoids do not require the same interpretation as free-living copepods or euphausiids. The primary environment of an hyperiid is its host. Its distribution is dependent on the host's distribution, which in turn is dependent on hydrological and trophic conditions. Hyperiid variations in abundance are statistically intractable and of little interest by themselves. Much more important is the study of the co-occurrence of an hyperiid and its host (which should be done preferably by counting them in the same samples). When this is undertaken (Metz, 1967; White & Bone, 1972; Laval, 1972; Thurston, 1977), the small figures found for hyperiids in plankton samples appear to be meaningful; the fluctuations of the amphipods are more or less closely related with those of their hosts. Thus despite the small numbers caught, a lunar cycle of abundance, reflecting that of its host the Leptomedusa *Phialidium,* was shown by Laval (1972) for *Lestrigonus schizogeneios.* Counts of *Vibilia armata* closely follow the variations of its host, the salp *Thalia democratica*; moreover, correlation is better with the oozoids (solitary form) than with the blastozooids (aggegate form), because the hyperiids cannot reproduce as fast as the latter form, with its asexual reproduction (unpubl. results). Many distributional studies of hyperiids considering the host–parasite relationship remain to be done.

VERTICAL MIGRATIONS

Marked vertical migrations are known in many species of hyperiids (see for example the comprehensive account of Thurston, 1976). Shulenberger (1978), however, has pointed out the inadequacy of data which are mostly not replicated, and most of these migrations are not well established. Very few authors, however, have related the vertical migrations with the hyperiid parasitic habits. Hardy & Gunther (1935) found similar patterns of distribution and migration between *Vibilia antarctica* and *Salpa fusiformis.* As the association between *Vibilia* and salps was not well known at that time, they only postulated such a relationship from their data. More recently Thurston (1976) also drew attention to the agreement between the vertical distributions of *V. armata* and *Salpa fusiformis,* noting that the amphipod is parasitic on salps. From his discussion it is apparent that he was inclined to think that hyperiids could follow their hosts to feed on them. In a later paper, Thurston (1977) expressed the same opinion concerning *Hyperia spinigera* and its host the medusa *Periphylla periphylla.*

Thus nobody appears to have asked a critical question: is not the apparent migration of hyperiids due only to the migration of their hosts? If one agrees with the views exposed in the foregoing pages, there could be no doubt that most juvenile hyperiids must move with the host on which they are attached. The so-called migration of the hyperiids would then in fact be that of their hosts, the hyperiids being passive. Why would the hyperiids spend much energy following food sources, if the sources go along with them? There seems to be considerable promise in studying hyperiid migrations from this point of view.

Adult hyperiids pose a more complex problem in the light of this hypothesis. They are not so dependent on hosts as the juveniles. For migrant species, the night is probably the more favourable period to wander in the

plankton. Owing to the vertical migration of planktonic animals, the upper layers are crowded with food organisms. Moreover darkness is propitious for host-seeking: bioluminescence (which is present everywhere in gelatinous zooplankton) would greatly facilitate the discovery of potential hosts. Thus the nocturnal period would be the time for an increase of activity among adult hyperiids, allowing them to feed and to find hosts. This is in agreement with the results of Thurston (1976) and Shulenberger (1978); day catches of hyperiids outnumber night catches, which may be explained by a greater net avoidance of the hyperiids not attached to a host.

ASSOCIATION ANALYSES

The danger of considering hyperiids independently of any host is illustrated in a recent study of niche separation among North Pacific hyperiids by Shulenberger (1979). Associations between hyperiids were searched using recurrent group analysis, from rank orders of abundance in plankton samples. Data on hosts were not taken into account. Although the paper contains an apparently sound ecological discourse, the results are biologically meaningless, because the data are irrelevant, and the sampling problems intractable. Hyperiids are associated with hosts, which constitute (together with the host's prey) their ecological niches. Instead of searching for associations between hyperiids and hosts, Shulenberger (1979) searched for associations among hyperiids themselves. Such associations, of secondary importance, are conceivable only if two hyperiids share the same host organism but use different resources. Although not unlikely, they still cannot be demonstrated from plankton counts. Grouping hyperiids by rank orders of abundance in samples may only reflect sampling artefacts or distributional hazards without ecological significance. Tranter (1977) used the computer programme MULTCLAS to obtain species groups of eastern Indian Ocean hyperiids. Although the emphasis is more on relationships of the species groups with water masses than in Shulenberger's study, the same criticisms may apply. Water masses are better characterized by the co-occurrence of certain species of siphonophores, salps, *etc.* than by one of their badly sampled parasites. For the time being, any ecological study of hyperiids should heavily rely on biological knowledge. The sampling method and the data analysis should come only as a second step.

With well conceived data, a statistical analysis may nevertheless disclose associations between hyperiids and zooplankton. In a principal component analysis of California Current zooplankton (Colebrook, 1977), the hyperiids stand in the centre of a well-defined group constituted only of radiolarians, ctenophores, thaliaceans, siphonophores, and medusae, *i.e.* all the gelatinous zooplankton (Fig. 8). This result, which was not perceived by Colebrook, is in my opinion a strong demonstration of the power of multivariate methods. It also proves, once again, that when dealing with hyperiids, biological knowledge is a prerequisite to the proper interpretation of statistical and ecological results. That hyperiids cluster with their hosts is also shown by a study of Ebeling *et al.* (1970), in which a principal component analysis places *Vibilia* spp. together with *Salpa fusiformis*. Data analyses can, however, only give presumptions of associations; the definitive proof rests with biological observations and experiments.

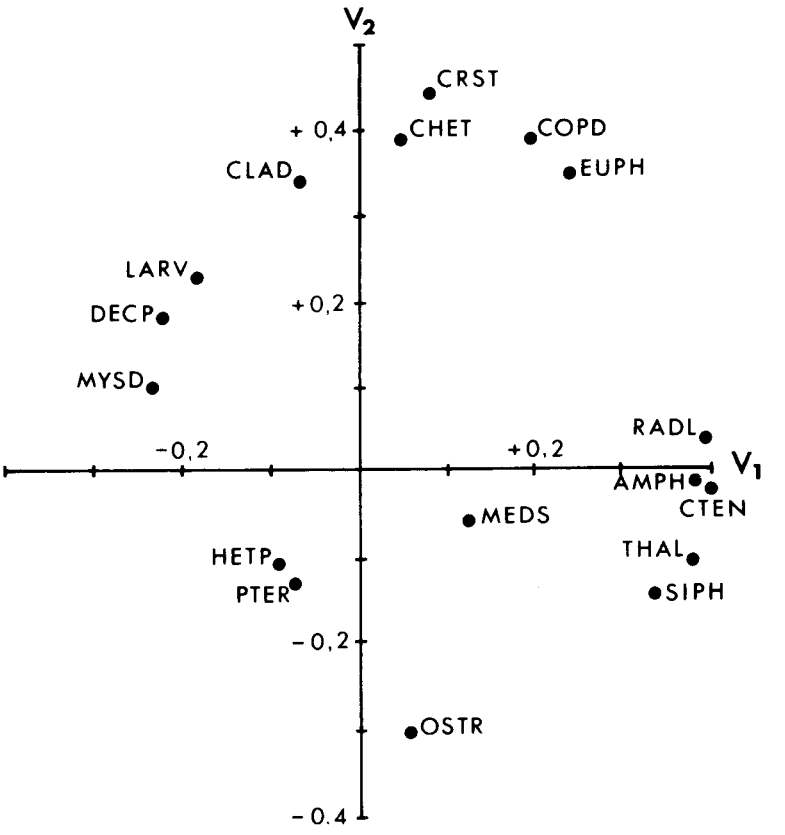

Fig. 8.—First 2 vectors (V_1, V_2) of a principal component analysis of zooplankton of the California Current, depicting the relationships of 17 taxonomic categories in 14 geographical subdivisions: the hyperiid amphipods are clearly associated with their gelatinous hosts; codes for taxonomic categories are as follows, AMPH, Amphipoda; CHET, Chaetognatha; CLAD, Cladocera; COPD, Copepoda; CRST, crustacean larvae; CTEN, Ctenophora; DECP, Decapoda; EUPH, Euphausiacea; HETP, Heteropoda; LARV, Larvacea; MEDS, Medusae; MYSD, Mysidacea; OSTR, Ostracoda; PTER, Pteropoda; RADL, Radiolaria; SIPH, Siphonophora; THAL, Thaliacea; (after Colebrook, 1977).

CONCLUSION

Although the association of hyperiids with other zooplankton has long been known, until now it was merely considered anecdotal. It is time to realize that hyperiids are not free-living amphipods occasionally found attached to other forms of the macroplankton. They are indeed crustacean parasitoids, which develop obligatorily on gelatinous hosts. Probably evolved from benthic ancestors, they have found on gelatinous macroplankton a pelagic substratum allowing the continuation of a benthic-like existence. Developing ingenious adaptations, they have overcome the principal

obstacle presented by the spatially discontinuous character of this peculiar structure. The liaison from one generation to the other is accomplished by the female, who herself secures the young to new hosts. For many species, the retention of embryonic characters, by hatching at a precocious stage, permits the appearance of specialized larval stages adapted to the process of host infestation. The diversion of the host's food provides a means of attaining the adult stage before killing the host. Behavioural adaptations, such as the limitation of the number of young deposited on a single host, maternal care, and mechanisms of immunity against the host's defences, ensure maximum success in host infestation. In the words of Pirlot (1932), by attaching themselves to macroplankton, they have conquered the pelagic spaces.

The pelagic realm is dominated by large numbers of calanoid copepods. This is, at least, the impression gained when examining plankton samples. Thanks to underwater observations, the picture of a clear ocean with only zooplankton patches is beginning to change (Hamner *et al.*, 1975). The importance of gelatinous zooplankton has been under-estimated owing to sampling problems with plankton nets. Salps, ctenophores, siphonophores, medusae, molluscs and colonial radiolarians form 'islands' in the ocean, providing sites of attachment, food and shelter for many animals. Their productions (secretions, mucous nets, egg-shells) also participate in this organic substratum. Hyperiids have adapted to this niche, by morphological, physiological, and behavioural specializations, many of which remain to be studied.

The importance of parasites has recently been re-assessed and it has been shown that, contrary to a common belief, parasitic species outnumber non-parasitic ones (Price, 1977). This may not surprise a marine biologist working with benthic forms, but it is still not apparent from the literature on pelagic animals. Any progress in this domain will be dependent on sampling techniques, but it may well be proved in the future that animal associations among the pelagic ecosystem are more important than previously thought.

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